

DISSERTATION

HIERARCHICAL BAYESIAN MODELS FOR
POPULATION ECOLOGY

Submitted by

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ABSTRACT

HIERARCHICAL BAYESIAN MODELS FOR POPULATION ECOLOGY

Models, by their definition, are abstractions of the systems they describe and require a delicate balance of inclusion of information with reduction. Hierarchical Bayesian models are well suited for ecological problems, because they facilitate the de-composition of highly complex ecological systems into lower dimensional elements. We can partition variability that arises from the ecological processes separately from variability that arises from sampling error, thereby rigorously accounting for uncertainty. In this way, we can better answer questions pertaining to the ecology of populations and aid in better management of their ecosystems.

Estimation of abundance is the central challenge in population ecology, and we begin this dissertation by addressing the problem of determining the population size of elk across multiple time and spatial scales during five winters. In Chapter 2, I build upon existing multi-state mark-recapture methods using a hierarchical Bayesian N -mixture model with multiple sources of commonly collected data on abundance, movement, and survival, to accurately estimate the abundance of a mobile population of elk on the winter range of Rocky Mountain National Park and Estes Park, CO.

Classification data are used in ecology to examine population trends through model-based theoretical approaches. For ungulates such as elk, wildlife managers use sex-ratios and stable age or stage distributions to assess population growth or decline. However, physical ambiguities and observer skill can lead to biased results. In Chapter 3, I develop two hierarchical models to address the sample bias that results when data are missing-not-at-random, which occurs when individuals are observed but not classified.

Forecasts are used to aid management to evaluate the probability that resource objectives will be met given different management actions. In Chapter 4, I develop a hierarchical model incorporating a discrete time, stage structured model assimilated with abundance and classification data, to provide forecasts under a variety of management actions to aid decision makers to meet objectives.

I use Bayesian hierarchical models that incorporate multiple sources of information to address common estimation problems that arise in population ecology. We are frequently interested in constructs and latent processes that are not necessarily observable in ecological systems. I use theoretical models of the underlying processes to extract information pertaining to populations and management goals. Compounding the challenge is that we must rely upon survey samples rather than complete census. I illustrate the utility of hierarchical Bayesian models using data on the population of elk (*Cervus elaphus nelsoni*) on the winter range of Rocky Mountain National Park in Colorado, USA.

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DEDICATION

For my mother, who never got to do her own

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CHAPTER 1

INTRODUCTION

1.1 Motivation and Overview

Ecological theory is primarily focused on the assessment of patterns of species distributions and abundance, as well as the mechanisms of interactions that drive those patterns. Effective monitoring of wildlife is vital for resource management of natural systems and requires quantitative information of population distributions, rates of harvest, survival, reproduction, movement, habitat, and space use (Lebreton et al., 1992; Ludwig et al., 1993). Assessment of these features along with their spatial and temporal variation is the hallmark of population ecology (Krebs, 2001). Conclusions about population dynamics and ecological processes are often inferred from samples rather than complete census of the population of interest and highlight the importance of rigorous statistical methods for estimation (Royle and Dorazio, 2008). Advances in survey design and analysis methods can improve population monitoring. This is particularly true for species in remote places where options for monitoring are constrained by policy and budget.

Overabundant ungulates throughout the United States can harm biological diversity of plant communities and impair ecosystem function. Wildlife managers have used a variety of methods for regulating ungulate populations including regulated hunting harvest, culling, and fertility control (Bradford and Hobbs, 2008; Ransom et al., 2012). Observations of excessive browsing by elk *Cervus elaphus nelsoni* on woody deciduous plants on the winter range of Rocky Mountain National Park during the last three decades motivated the development of the Elk Vegetation Management Plan (National Park Service, 2007). The goal of the plan is to reverse degradation of plant communities by reducing elk abundance and by protecting

stands of vegetation from browsing (Singer et al., 1998; Zeigenfuss et al., 1999; Lubow et al., 2002; Binkley et al., 2003; Schoenecker et al., 2004). Implementing the Management Plan requires comparing estimates of the elk population size to ecologically sound targets, which requires reliable census and modeling approaches for monitoring the state of the elk population. Several estimation problems have arisen from altering survey methods and because these data are collected by multiple government agencies.



Figure 1.1: Elk crossing the Big Thompson River in Moraine Park in Rocky Mountain National Park on November 6, 2014. Photograph by Alison C. Ketz

1.2 Chapter Introductions

This dissertation was prepared in manuscript format in accordance with the requirements of the Graduate School of Colorado State University. The text is divided into four chapters, including this introduction. The format of each chapter follow most of the guidelines of the target journal for which they were prepared or submitted. In some cases, text that was omitted for publication due to page and word limitations were included in the main body of the text for this dissertation. Chapter 4 has been published (November 2016).

Estimation of abundance forms the central challenge in population ecology, because populations change over time and space, and because complete census of populations is not possible. Detection of individuals or groups inside the study area must be adjusted to correct for the bias that occurs when individuals are present in a study area but not observed. Variability in the distribution of mobile species confounds efforts to estimate detection. For a large free-ranging species such as elk, aerial surveys are the gold standard used to survey populations, particularly in geographic regions with harsh terrain. However, aerial surveys can be prohibitively expensive and dangerous. Estimating abundance with ground based survey methods can have practical advantages, but observer error and temporary emigration must be accounted for. In Chapter 2, we build upon existing multistate mark-recapture methods using a hierarchical Bayesian N -mixture model with multiple sources of commonly collected wildlife data, to estimate the abundance of elk in Rocky Mountain National Park. We use a state-space approach to model animal movements using telemetry data to approximate the number of marked animals present within a fixed conservation area at any observation period, thereby accounting for a frequently changing number of marked individuals. We then combined this movement model with an abundance estimator in an N -mixture model to obtain population estimates throughout winter seasons across five years, thereby assessing temporal variation along the winter range at multiple time scales. We demonstrate the improved inference of our method compared with existing estimators of abundance. Data collected on

abundance, movement and survival are commonplace in managed ecosystems. By combining all of these sources of information we improve inference of abundance estimates, which in turn, aid in management decisions.

Classifications are used to examine population trends of species and communities through modeling approaches including sex ratios, stable age/stage distributions, and discriminant analyses. Assignment of individuals to a category can prove challenging for numerous factors, including physical ambiguities and varying observer skill. When individuals are observed but not classified, these “partial” observations must be modified to include the missing data mechanism to avoid spurious inference. In Chapter 3, we developed two hierarchical Bayesian models to overcome the assumption of perfectly observed mutually exclusive categories in the multinomial distribution of categorical counts, when partial classifications are missing or unknown. Both models incorporate auxiliary information to adjust the posterior distributions of the proportions of sex and stage classes. We performed a simulation to show the bias that results when partial observations are ignored and estimation of demographic ratios can be effected. We developed multiple approaches that use a nested multinomial structure to account for partially observed data that were missing not at random for classification counts.

Bayesian hierarchical models can assimilate data to provide forecasts, resulting in probabilistic predictions of future states of park ecosystems accompanied by rigorous estimates of uncertainty. We discuss a novel approach for using these forecasts to aid decision makers who need to evaluate the probability that National Park Service goals will be met given different management actions, including the null model of no-action. Forecasts from a discrete time, stage-structured population model assimilated with annual census and sex and age classifications are being used annually to help park managers decide on actions needed to meet goals for elk and vegetation. In particular, park managers were able to determine the probability that the elk population would fall within a desired population range, which led to both population reduction actions and no action depending on the year of interest. Moreover, this approach allowed multiple survey methodologies to be incorporated into a

single model with associated estimates of uncertainty. Models like this one are especially useful for adaptive management where continuous improvement in models and data result in long-term improvement in the wisdom of policy and management.

1.3 Mathematical Notation

Conventional notation was used in this dissertation, however, for clarity I define all notation used in this work as follows. Matrixes are denoted in bold capital letters. Vectors are bold lowercase letters. An exception are population totals, which are typically denoted with a capital N for single observations and bold font is used for multiple observations in both matrixes and vectors. Probability distributions are denoted with brackets $[]$. Subscripts appearing in text font are labels, in italics they are indexes of vectors or matrixes. The transpose symbol is given by a apostrophe slash on the right hand side of a vector or matrix. All vectors are assumed column vectors unless otherwise altered with the transpose symbol.

CHAPTER 2

ESTIMATING ABUNDANCE OF AN OPEN POPULATION WITH AN *N*-MIXTURE MODEL USING AUXILIARY DATA ON ANIMAL MOVEMENTS ¹

Estimating abundance and explaining fluctuations in abundance form the central challenges in population ecology and wildlife management (Seber, 1982). The growth or decline of populations over time reflects numerous factors, including movement and survival. We developed a model to simultaneously estimate abundance, survival, and movement probabilities, to address these challenges and to inform decisions on managing animal populations within areas defined by fixed jurisdictional boundaries. Large mobile animals can move into and out of these areas, creating challenges for abundance estimation and hence, complicate decisions on population management.

It is vital that population estimates account for the inevitable bias that results from animals that are present but not seen. Failing to account for detectability means that differences in population estimates from year to year may result from errors in observing the population rather than from differences in the population itself. Many methods have been proposed to account for the problem of imperfect detection in estimates of animal abundance. These include mark-recapture (Nichols, 1992; Pollock, 1982; Kendall et al., 1997), removal sampling (White and Leffler, 1982), and distance sampling (Buckland, 2001). All of these methods use design based procedures for estimating the probability of detecting

¹Ketz, A. C., Johnson, T. L., Monello, R. J., Mack, J., George, J. L., Kraft, B. R., Wild, M. A., Hooten, M. B., & Hobbs, N. T., Estimating abundance of an open population with an *N*-mixture model using auxiliary data on animal movements.

individuals given that they are present. Detection probabilities, in turn, are used to account for individuals that are present but not counted, thereby correcting for “undercounting” bias.

There are many sources of variability that have been accounted for in mark-recapture estimators, including individual heterogeneity, environmental heterogeneity, time dependence, behavior, and combinations of all of these (Kendall, 1999; Borchers et al., 2002). The estimation of the detection probability can be confounded by the fact that only a proportion of individuals in a population is available for sampling at any given time (Kendall, 1999). Many mark-recapture estimators have been developed to adjust for mobility of species because movements in space can be substantially broader than the geographic regions that are surveyed. Temporary emigration can lead to biased estimates of abundance, resulting from underestimates of the probability of detection (p) and a corresponding overestimation of the total population size (N) (Nichols and Kendall, 1995; Kendall et al., 1997). Different types of movement can lead to a variable number of individuals that are available to sample and may confound estimates across multiple surveys (Kendall, 1999). Knowledge of the total population that uses these static regions can help inform management actions that target animals within fixed boundaries.

We developed a hierarchical Bayesian model for estimating population sizes in a mark-recapture framework, using an N -mixture model coupled with location data on animal movement and survival. The method provides inference based on the posterior distribution of the average abundance of animals in a sequence of counts within a specified area without assuming that the area is closed to immigration, emigration, or mortality. We use very high frequency (VHF) telemetry collars and subsequent location information collected on a weekly timescale to model the temporary movement patterns of individuals into and out of the study region to estimate abundance in an open population (Chandler et al., 2011; Ivan et al., 2013; Dail and Madsen, 2011) without making assumptions regarding individual home ranges or spatial distributions (Royle et al., 2014).

We used a model-based approach to estimate overall average abundances across multiple years and simultaneously estimate demographic parameters that provide important information about the state of the surveyed population. We estimated survival probabilities on weekly and annual time scales and we estimated transition probabilities that reflect movements among multiple areas within the surveyed region, which allowed us to assess the connectivity of various subgroups of the population. Our novel approach makes use of multiple sources of commonly collected data, thereby providing a complete summary of the state of the population during a specific period of time.

2.1 Materials and Methods

2.1.1 Overview of modeling approach

Locations obtained from VHF collars are prone to errors and missing observations, motivating the use of a state-space approach to obtain posterior distributions of the true locations. We separate observed telemetry location data from an underlying true location of each collared individual. A general state space approach can be described as the conditional probability of observations (Y) given a true state (X) and a set of parameters governing the uncertainty with the data (θ_d),

$$[Y|X, \theta_d], \tag{1}$$

where the brackets denote a probability distribution. We can link our knowledge of the ecological system to the observations using a model for the latent state (X) and parameters

(θ_p) governing its behavior such that

$$[X|\theta_p]. \quad (2)$$

We separated an underlying Markovian movement process model from a data model specified for location observations. Using this hierarchical structure, we were able to estimate the number of marked individuals that were available in the sample area during any week we surveyed the population. The movement model informs the true, unobserved locations of marked individuals, which allows us to know, with estimates of uncertainty, the true number of marked individuals within the study area.

We coupled the movement model with a mark-recapture estimator of independently collected count data from repeated surveys. The observed counts (n) can be modeled with a conditional probability distribution that depends on the total population size (N) and some function of detectability ($f(X)$), that we derived from the movement model true states. In general, a model combining the movement with census is described as

$$[n|N, f(X)]. \quad (3)$$

The data (n) consist of counts of the total number of individuals within the survey region as well as observations of the number of marked individuals within encountered groups. We also used additional secondary information to account for imperfectly recorded resighted marks, by calibrating the resights with telemetry data collected to verify this separate detection process. We combined the estimates of the true number of marked individuals within the region of interest with the estimated number of resighted marks, to determine the probability of detecting an individual in an N -mixture model (Equation 3). We used a Bayesian approach implemented in JAGS (Plummer, 2014a) to approximate posterior distributions of model parameters (see supplement).

2.1.2 Model development for marked individuals

We first considered the general scenario of repeatedly sampling a population of N individuals for $t = 1, \dots, T$ surveys. A subset of the population has been subjected to capture, in which individuals representative of the population are marked, and subsequently recaptured or resighted during T occasions.

We know that the total population size will likely change between surveys because of temporary emigration, immigration, and mortality. Using a hierarchical structure, we were able to capture sampling error resulting from temporal variation in abundance within the study area, as well as accounting for observation error resulting from failing to count animals that were present but not observed. Thus, a sample of n_t individuals is distributed as a binomial random variable such that

$$n_t \sim \text{binomial}(N_t, p_t) \quad (4)$$

$$N_t \sim \text{Poisson}(\mu) \quad (5)$$

$$\mu \sim \text{gamma}(\alpha, \beta), \quad (6)$$

where N_t is the total population size during sample t and μ is the overall average number of individuals that use the study area during the sampling intervals. The detection probability $p_t = \frac{R_t}{M_t}$ is defined as the ratio of the number of resighted marks (R_t) out of the total number of marked individuals (M_t), during the t th survey, similar to the classical Lincoln-Petersen estimator (Otis et al., 1978; Seber, 1982). Auxiliary data must be used to determine p_t to avoid identifiability problems, because both N_t and p_t are unknown.

We explicitly modeled the movement behavior of marked individuals using location data collected with telemetry (VHF), and, in turn, we estimated the true number of marked individuals available for sampling during census. We made the assumption that closure only

applies on the time scale of the location data intervals. Additional assumptions include that detection does not vary with any environmental heterogeneity, and that individuals do not alter behavior resulting from the initial capture.

2.1.3 Elk in Rocky Mountain National Park

The method we offer is general, and could apply to any species that moves in and out of a static study area during repeated surveys across a season. We developed the approach to provide estimates of population sizes corresponding to a fixed spatial domain targeted by management. Estimates reflect the number of individuals that use this domain, rather than a spatially constant population size, because environmental impact is based on the use of the conservation area.

We illustrate the approach using data on the wintering elk population in the Estes Valley, which consists of lower elevation areas on the eastern side of Rocky Mountain National Park (RMNP) and in the adjacent town of Estes Park, Colorado (EP). Management decisions based on abundance are made annually and require an estimate for the average number of elk using the park during the winter.

Aerial survey methods were used to survey elk in RMNP for twenty years (1994-2014), however, the high costs and dangerous conditions of flying over the eastern slope of the Rocky Mountains during the winter motivated a change to ground survey methods. We used weekly VHF telemetry data collected throughout the winter months to determine the number of marked animals available in the region during ground surveys, where total counts of groups and counts of marked individuals were made along 10 road transects to obtain the abundance of elk in both RMNP and EP.

We developed this model to understand movements of elk across static park boundaries, as well as to develop a ground-based survey method that could be repeated multiple times during the winter season to understand temporal variation in elk abundance on the winter range within RMNP and EP.

2.1.4 Data description

Approximately twenty volunteers drove road transects on the winter range of RMNP and EP. The volunteers recorded counts (y_{n_t}) of elk groups, as well as the number of collared elk present (m_t) during three days during the first or second week of each month of winter (November-March). The average total number of elk per day within each week, rounded to the nearest integer, (n_t) were used as data in the N -mixture model of equation 4 to account for sampling variability within survey weeks.

We used the weekly ground telemetry locations of approximately 150 collars that were deployed by the National Park Service, and Colorado Parks and Wildlife (Figure 2.1) to correct for animal movements across park boundaries in the model described below. The dates of collar deployment for each collar are known.

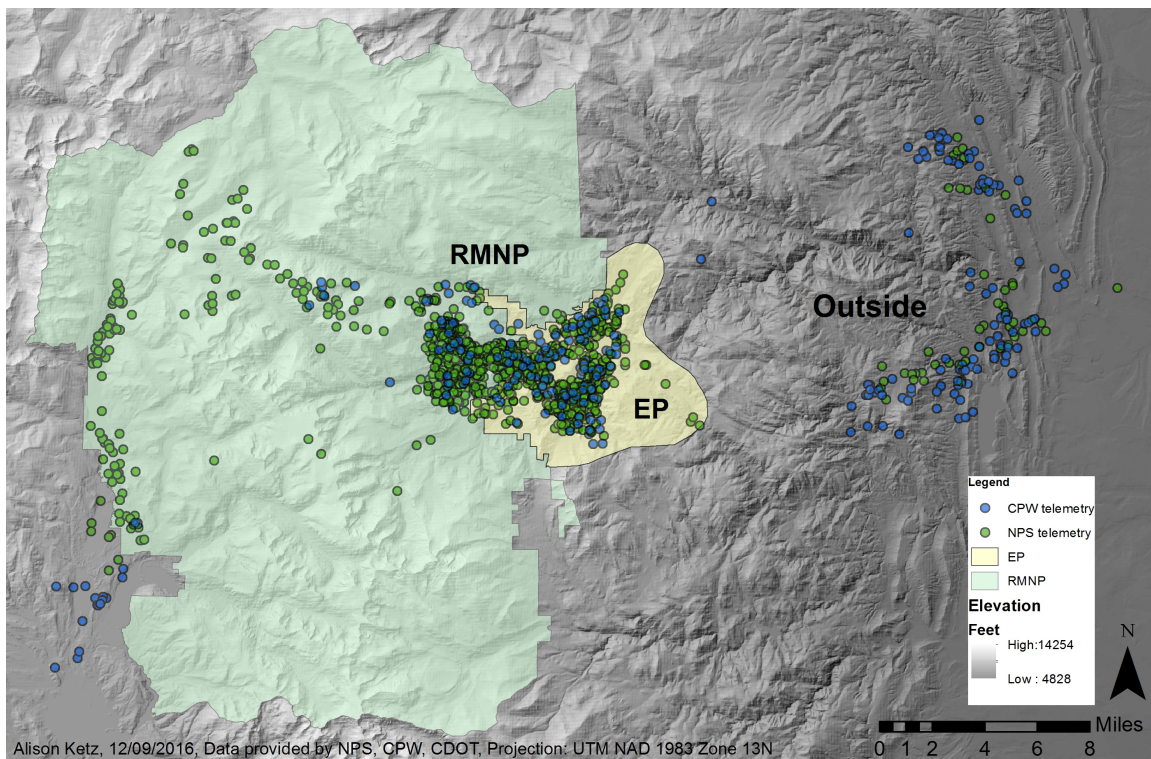


Figure 2.1: Observed telemetry location data over time are represented by points. The green area represents Rocky Mountain National Park (RMNP) and the yellow region represents the town of Estes Park (EP). Telemetry locations were collected by two government agencies, the National Park Service (green points) and Colorado Parks and Wildlife (blue points).

2.1.5 Movement Model

Ideally, we would know the true locations of these collared elk every week, although realistically, the true state of the collared elk location was not always observed perfectly. We used a hierarchical, state space model to account for the movement of elk among three possible locations. We also incorporate observations of the marked individual’s status, alive or dead.

First, we describe a process model of the underlying true condition of the collared elk. We define a vector of seven mutually exclusive categories, or “true states” (Table 2.1). The three location categories indicate that the i th elk is either alive or dead within RMNP, EP, or outside the study area (generally the foothills). These areas can be seen in Figure 2.1 with all telemetry observations throughout the winters from 2011-2016.

Table 2.1: We define a vector $\mathbf{x}_{i,t}$ with a 1 in one of seven mutually exclusive true states of the i th collared elk during the t th week of winter, with zeros elsewhere. We define a vector $\mathbf{y}_{i,t}$ with a 1 in one of ten mutually exclusive observed states of the i th collared elk during the t th week of winter, with zeros elsewhere.

Element j	Definition
$x_{1,t}$	Alive in RMNP
$x_{2,t}$	Alive in EP
$x_{3,t}$	Alive outside of Estes Valley
$x_{4,t}$	Dead in RMNP
$x_{5,t}$	Dead in EP
$x_{6,t}$	Dead outside of Estes Valley
$x_{7,t}$	Out of study
$y_{1,t}$	Observed alive in RMNP
$y_{2,t}$	Observed alive in EP
$y_{3,t}$	Observed alive along RMNP/EP boundary
$y_{4,t}$	Observed alive outside the Estes Valley
$y_{5,t}$	Observed alive, but no information on location is obtained
$y_{6,t}$	Observed dead in RMNP
$y_{7,t}$	Observed dead in EP
$y_{8,t}$	Observed dead outside the Estes Valley
$y_{9,t}$	Unobserved
$y_{10,t}$	Out of study

$$\Theta = \begin{pmatrix} \phi\pi_{1,1} & \phi(1-\pi_{2,2})\pi_{2,1} & \phi(1-\pi_{3,3})(1-\pi_{3,2}) & 0 & 0 & 0 & 0 \\ \phi(1-\pi_{1,1})\pi_{1,2} & \phi\pi_{2,2} & \phi(1-\pi_{3,3})\pi_{3,2} & 0 & 0 & 0 & 0 \\ \phi(1-\pi_{1,1})(1-\pi_{1,2}) & \phi(1-\pi_{2,2})(1-\pi_{2,1}) & \phi\pi_{3,3} & 0 & 0 & 0 & 0 \\ (1-\phi)\pi_{1,1} & (1-\phi)(1-\pi_{2,2})\pi_{2,1} & (1-\phi)(1-\pi_{3,3})(1-\pi_{3,2}) & 0 & 0 & 0 & 0 \\ (1-\phi)(1-\pi_{1,1})\pi_{1,2} & (1-\phi)\pi_{2,2} & (1-\phi)(1-\pi_{3,3})\pi_{3,2} & 0 & 0 & 0 & 0 \\ (1-\phi)(1-\pi_{1,1})(1-\pi_{1,2}) & (1-\phi)(1-\pi_{2,2})(1-\pi_{2,1}) & (1-\phi)\pi_{3,3} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 1 & 1 \end{pmatrix}. \quad (7)$$

Element	Definition
$\pi_{1,1}$	Probability that an animal in RMNP at time t stays in RMNP at time $t + 1$
$\pi_{1,2}$	Conditional on the animal moving from RMNP, it moves to EP
$\pi_{2,2}$	Probability that an animal in EP at time t remains in EP at time $t + 1$
$\pi_{2,1}$	Conditional on the animal moving from EP, it moves to RMNP
$\pi_{3,3}$	Probability that an animal outside the Estes Valley at time t remains outside at $t + 1$
$\pi_{3,2}$	Conditional on the animal moving from outside the Estes Valley, it moves to EP

Figure 2.2: The matrix Θ combines transition probabilities ($\pi_{i,j}$) for the i th location during week t and j th location during week $t + 1$ to describe the movement process between RMNP, EP, and whether individuals move outside the study area or enter the study area.

We used a vector of the true states ($\mathbf{x}_{i,t}$) to represent the true, unobserved location and condition of the i th collared animal at week t of winter. Individuals were denoted as out of the study if they were not yet collared or had died during a previous week of winter. A matrix of across winter histories of the state of the i th individual, \mathbf{X}_i , consists of a collection of the true state vectors across all time points. Thus, each column of \mathbf{X}_i represents a weekly time point for $i = 1, \dots, I$ collared elk. We assume a Markovian movement model, such that the probability of an elk moving from one state to another depends on the state of the elk during the previous point in time. The probabilities of the individual moving among states are described in Figure 2.2. We define a constant weekly survival probability ϕ independent of movement and inclusive of harvest and incorporate this probability into the transition matrix. A multinomial distribution was used to model the true latent state of the animal at

time $t - 1$ where

$$\mathbf{x}_{i,t} \sim \text{multinomial}(1, \Theta \mathbf{x}_{i,t-1}), \quad (8)$$

using the transition matrix Θ (Figure 2.2).

If we could actually observe these true states of the elk, then estimating the movement and abundance would be unnecessary because we would already know the status of the population without uncertainty. However, there is uncertainty in the observation process – the true state (Table 2.1) was related to the observed state (Table 2.1) through telemetry data.

$$\mathbf{D} = \begin{pmatrix} p_s p_v p_d & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & p_s p_v p_d & 0 & 0 & 0 & 0 & 0 \\ p_s p_v (1 - p_d) & p_s p_v (1 - p_d) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_s p_v & 0 & 0 & 0 & 0 \\ p_s (1 - p_v) & p_s (1 - p_v) & p_s (1 - p_v) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_s & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & p_s & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & p_s & 0 \\ 1 - p_s & 1 - p_s & 1 - p_s & 1 - p_s & 1 - p_s & 1 - p_s & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}. \quad (9)$$

Parameter	Definition
p_s	Probability that the individual is observed.
p_v	Conditional on being observed, the probability that information on location is obtained.
p_d	Conditional on being observed with location information, the probability if it is in RMNP or EP.

Figure 2.3: Detection probabilities are defined for the observations of VHF collared elk and combined in the detection matrix \mathbf{D} .

A multinomial distribution was used to model the set of possible outcomes of observable states that arise from the underlying latent process. We link the observations of the state of

the collared elk to the true states of the elk using a detection matrix \mathbf{D} such that

$$\mathbf{y}_{i,t} \sim \text{multinomial}(1, \mathbf{D}\mathbf{x}_{i,t}), \quad (10)$$

where the detection matrix and probabilities are defined in Figure 2.3.

The number of marked individuals that could possibly be seen during ground census were calculated using the sum of the state vectors for the two geographic regions of interest during week t . The true number of collared elk in RMNP is $\sum_i x_{1,i,t}$ and for EP it is $\sum_i x_{2,i,t}$. Recall that $x_{1,i,t}$ represents whether the i th collared elk during the t th week of winter is either alive and in RMNP (1) or not (0). Similarly, the state of the elk with regards to EP ($x_{2,i,t}$) is either a 1 (present) or 0 (not present). We defined the number of marks (M_t) equal to the summation of the state vectors for the corresponding region of interest. Thus, the denominator for the detection probability in Equation 4 for the elk in RMNP is $\sum_i x_{1,i,t}$ and similarly, the denominator in the detection probability for the elk in EP is $\sum_i x_{2,i,t}$. Movements between RMNP and EP are not independent because these states are mutually exclusive. However, because we explicitly model the movement across these regions, we do not need to incorporate the correlation between the abundance estimates for each area.

2.1.6 Calibration model for resights

Perfectly observed resights of collars is a typical assumption of mark-recapture estimators. Estimates of population sizes are quite sensitive to violations of this assumption. One of the strengths of the Bayesian approach for learning about model parameters is that it is straightforward to alter the model to accommodate idiosyncrasies in the data, in this case, the failure to observe all marks that were present. The National Park Service deployed brown telemetry collars within RMNP to make collars less visible to park visitors. However, this meant that observers counting elk were not always able to see all collars present in a group. There were obvious errors in the number of marks observed during the ground count (m_t) leading to potentially serious biases in estimates of population size. This was particularly

problematic when the elk were aggregated into large groups, which is common for calf and cow herds during winter. We collected data and developed a calibration model to account for the collars that were present but overlooked.

We observed “true” counts of collars using the VHF signal of collared elk within sighted herds, simultaneous with the ground count surveys. These locations were collected by experienced staff in extremely close physical proximity to the sighted herds to minimize errors. We assumed that the detection process depended on the size of the herd. The higher the number of elk in a group, the less likely that all of the collars were correctly counted.

We used an N -mixture model approach because we know the true number of marked elk within a sighted group from the telemetry signal. Let $z_{t,j}$ be the true number of marks in the j th observed herd within week t of winter. Also note that the observed ground count ($y_{\text{count},t}$), either in EP or in RMNP is the sum of all the herds counted in each area ($y_{\text{count},t} = \sum_j n_{\text{herd},t,j}$). The proportion of resighted collars was estimated as a function of elk herd size. The model for the resights with $l = 1 \dots L$ observed true telemetry marks (z_l) is

$$m_l \sim \text{binomial}(z_l, g_l(\beta_0, \beta_1)), \quad (11)$$

$$g_l(\beta_0, \beta_1) = \frac{\exp(\beta_0 + n_{\text{herd},l}\beta_1)}{\exp(\beta_0 + n_{\text{herd},l}\beta_1) + 1}, \quad (12)$$

$$\beta_0 \sim \text{normal}(0, 5), \quad (13)$$

$$\beta_1 \sim \text{normal}(0, 5), \quad (14)$$

where β_0 and β_1 were estimated using data consisting of the true marks that were collected with telemetry during a subset of surveys, in both RMNP and EP. A vague prior distribution of $\text{normal}(0, 5)$ was used for the coefficients (β) in the calibration model. We applied the

coefficients from this model, estimated from a single year of data (2014), to all of the surveyed groups within the five years of the study. We calculated the posterior distributions of the calibrated marks, which were derived parameters calculated using the total number of collars within RMNP and within EP that were summed across the transects within each area as

$$z_{k,t,j} = \frac{m_{k,t,j}}{g_{k,t,j}(\beta_0, \beta_1)}, \quad (15)$$

$$z_{k,t} = \sum_j z_{k,t,j}, \quad (16)$$

for the j th herd, during the t th week of the $k = 1, \dots, 5$ years. The moment matched (Hobbs and Hooten, 2015) posterior mean and standard deviation of the maximum number of collars within survey weeks was used in the prior distribution for the number of resights for the numerator in the detection probability in Equation 4. We chose the maximum because multiple day surveys often reported multiple sightings of the same collars within a single week, but additional collars were also seen on certain days.

Thus, the probability of detection for the t th week of winter in RMNP (Eq. 4) was

$$p_{\text{RMNP},t} = \frac{z_{\text{RMNP},t}}{\sum_i x_{1,i,t}}, \quad (17)$$

and similarly, the detection probability for the elk in EP (Eq. 4) was

$$p_{\text{EP},t} = \frac{z_{\text{EP},t}}{\sum_i x_{2,i,t}}, \quad (18)$$

with a prior on the corresponding $z_{\text{RMNP},t}$ and $z_{\text{EP},t}$ of

$$\mathbf{z}_t \sim \text{gamma} \left(\frac{z_{\text{mn},k,t}^2}{z_{\text{sd},k,t}^2}, \frac{z_{\text{mn},k,t}}{z_{\text{sd},k,t}} \right). \quad (19)$$

As expected, we found an inverse relationship between herd size and collar detectability (Figure 2.5). We assumed all observers were equally skilled and data were not collected to capture variability among observers because the pool of volunteer ground counters was large and changed throughout the surveys.

2.1.7 Model Fitting

Standard uniform prior distributions were chosen for movement, survival, and detection probabilities. One ground count survey from the second year of study was omitted from the analysis due to inaccurate counting. The prior distribution for the average across winter mean of elk in both RMNP and EP was specified as $\text{gamma}(3, .01)$, based on prior information from previous years of study that the average number of elk approximately ranged in the low to mid hundreds, in the range of 200 to 400 individuals in either area (Ketz et al., 2016).

The full hierarchical Bayesian model, with the corresponding directed acyclic graph, as well as the joint and posterior distributions are provided in Appendixes 5.1.1 and 5.1.2, respectively. We verified that parameters could be accurately recovered during model fitting using simulations based on known parameters. The model was fit using JAGS (Plummer, 2014a) with the ‘dclone’ package (Sólymos, 2010) for parallel computation of the ‘rjags’ package (Plummer, 2013) in R (R Core Team, 2016). Three chains consisting of 200,000 Markov chain Monte Carlo iterations with a burn-in of 50,000 iterations were generated.

Trace plots, ACF plots, and the Gelman-Rubin (Gelman et al., 2014) diagnostics indicated convergence of virtually all of the marginal posterior distributions of model parameters and latent states. Convergence problems arose for the approximation of the posterior distributions of three of the model parameters, namely for the derived probability of detection from one of the months during the first year of study, and for two of the derived monthly probabilities of detection during the second year of the study. However, in all instances, the across winter average population size of elk successfully converged, so inference for this parameter is valid. After one monthly survey from the third year of the study was removed, posterior predictive checks showed no evidence of lack of fit (Gelman et al., 2014) for all years.

2.1.8 Model Comparisons

We considered three additional models of abundance. Ideally, we could obtain the abundance of this population without using mark-recapture data for cost-effective future ground surveys. Therefore, we modeled the ground count data in an unmarked context using the Dail-Madsen model in the Bayesian framework (Dail and Madsen, 2011). We specified the 10 road transects as sites for spatial replication and used 15 surveys of counts from each winter across the years to obtain the average number of individuals in the combined survey region (RMNP and EP) for each year.

We modeled the mark-recapture telemetry data with the Jolly-Seber model, useful only for model comparison because the collars were deployed in a Cormack-Jolly-Seber context and initial captures were not necessarily fully random nor consisted of marks of all individuals in sighted/resighted groups. We compared the results of our N -mixture model with the Jolly-Seber approach by approximating distributions of abundances across winter for each year separately using the Bayesian occupancy parameterization of the Jolly-Seber model (Royle and Dorazio, 2008; Kéry and Schaub, 2011).

We then developed a mark-recapture N -mixture model similar to Pollock’s robust design in a Bayesian framework (Pollock, 1982; Kendall et al., 1997), without adjusting the number of marked individuals using the state-space model of telemetry data. We specified a primary sampling period for each of the five months of winter, in which temporary emigration was permitted. We assumed closure within the ground survey weeks (secondary samples) where we used repeated count surveys and used the proportion of re-sighted marks to the total number of marks for the detection probability. We did not correct the number of marks available for sampling using the auxiliary telemetry data. All of these models were approximated using MCMC and standard diagnostics indicated convergence of all posterior distributions.

2.2 Results

The estimated population sizes in RMNP and EP were substantially lower than the historical estimates of overabundant elk on the winter range (Ketz et al., 2016; Hess, 1993; Lubow et al., 2002) (Figure 2.4 and Table 2.2). The median of the posterior distribution of the population size in the study area as a whole ranged from a low of 488 individuals in 2012 with an equal-tailed Bayesian credible interval (BCI = 462, 515), to a high in 2014, with a median of 825, (BCI = 747, 918) individuals (Table 2.2 and Figure 2.4).

The number of elk that used RMNP more than doubled between 2012 and 2013, from 171 (BCI=158, 187) to 422 (BCI=372,478) individuals. Increases in the population on this time scale were more likely to result from the fluid connectivity of the sub herds that also use other areas, such as EP or the foothills during the winter than from increased recruitment of the same animals within RMNP. These results highlight the fact that movement between RMNP, EP, and the foothills is an important process that must be accounted for during abundance estimation.

Table 2.2: Five years of the average number of elk on the winter range from 2012 through 2016 for RMNP (μ_{RMNP}), EP (μ_{EP}), and the Estes Valley as a whole (μ_{VAL}). The right two columns represent the 0.025 and 0.975 quantiles of the marginal posterior distributions of the estimated parameters.

Parameter	Year	Mean	Median	SD	0.025	0.975
μ_{RMNP}	2011	321	321	15.1	293	352
	2012	171	171	7.2	158	187
	2013	423	422	27.1	372	478
	2014	420	418	42.1	344	508
	2015	244	238	28.3	207	319
μ_{EP}	2011	222	222	7.7	207	238
	2012	317	317	11.4	295	339
	2013	306	306	13.9	280	334
	2014	407	406	14.3	380	436
	2015	379	379	16.4	348	412
μ_{VAL}	2011	544	543	16.9	511	577
	2012	488	488	13.5	462	515
	2013	729	729	29.0	674	788
	2014	827	825	43.7	747	918
	2015	623	619	32.2	573	702

Posterior distributions of the process model parameters were generated for each year of the study separately, and showed little influence from the prior distributions (Appendix 5.1.3, Figures 5.2,5.3,5.4). The weekly survival probabilities were transformed into annual estimates of survival, using the transformation ϕ^T (Noon and Sauer, 1992), where T was the number of weeks of winter telemetry observations within each year. Median annual survival probabilities increased during the first four years of the study, and decreased during the last year (Table 2.3).

Movement probabilities were consistent among all years and had a similar trend within years (Appendix 5.1.3, Table 5.2). For example, in 2015, collared individuals that were in RMNP were more likely to remain (median $\pi_{11} = 0.88$ (BCI = 0.86,0.9)) than they were to leave (median $1 - \pi_{11} = 0.12$ (BCI = 0.1,0.14)). Similarly, the median probability that a collared individual that was in EP at time t (π_{22}), would stay was 0.85 (BCI = 0.83,0.88). Although collared individuals were more likely to remain in their location based on these

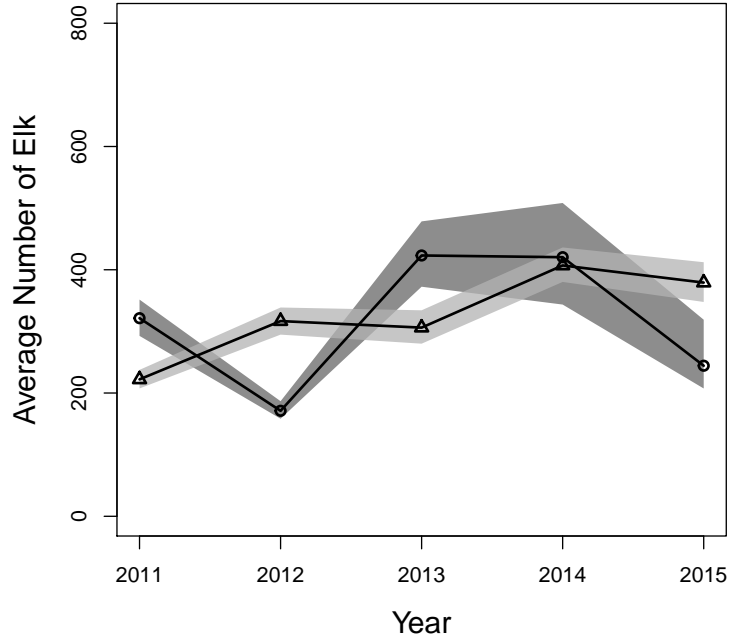


Figure 2.4: The median number of elk using Rocky Mountain National Park, μ_{RMNP} (circles), and in the town of Estes Park, μ_{EP} (triangles), shows the population during five winters. The 95% Bayesian credible intervals for RMNP (dark gray) and EP (light gray) are the shaded regions.

transition probabilities, movement between these areas, as well as outside of the study region was occurring because the mass of probability ($> .999$) in the posterior distributions of movement parameters ($\boldsymbol{\pi}$) did not include 1.

The probability of detecting a collared individual (p_s) decreased throughout the years of the study (Appendix 5.1.3, Table 5.1). Low probabilities of detecting the marked individuals (p_s) justifies the use of the state space approach for modeling telemetry data, where missing data are treated as unknown parameters and the posterior distributions of the true locations can be approximated. After an individual was detected, information about the location of that individual was likely obtained with posterior median detection probabilities $p_d = p_v = 1$.

We found an inverse relationship between herd size and collar detectability, such that the probability of missing marks within a sighted group decreased by -0.0099 , ($\text{SD}=0.0041$)

Table 2.3: Annual survival (ϕ^T) posterior distribution summary statistics derived from a constant weekly survival estimated from the weekly telemetry data. The right two column headings represent the 0.025 and 0.975 quantiles of the marginal posterior distributions.

Year	Mean	Median	SD	0.025	0.975
2011	0.866	0.871	0.047	0.763	0.943
2012	0.927	0.929	0.025	0.872	0.968
2013	0.927	0.929	0.021	0.880	0.963
2014	0.971	0.973	0.014	0.937	0.992
2015	0.961	0.964	0.017	0.922	0.987

as herd size increased with each additional elk (Figure 2.5). The observed proportions of collared elk accurately detected during ground counts in both RMNP and EP show high variability in sightability, ranging from 0.13 to 1.0.

Summary statistics of the posterior distributions for the average number of elk in the winter range of the Estes Valley showed the altered inference that occurred when different models and different data of the same population were used (Table 2.4). The Jolly-Seber model, which only considered abundance using the telemetry data, had the lowest mean population sizes, with medians below the ground count population totals. The open population Dail-Madsen model posterior means, using only the ground count data, were nearly nine times greater than the Jolly-Seber model posterior means. When observation error of the telemetry data were ignored, the posterior means of the average overwinter number of elk were more than three times greater than the posterior means using the state-space model of movement of the telemetry data.

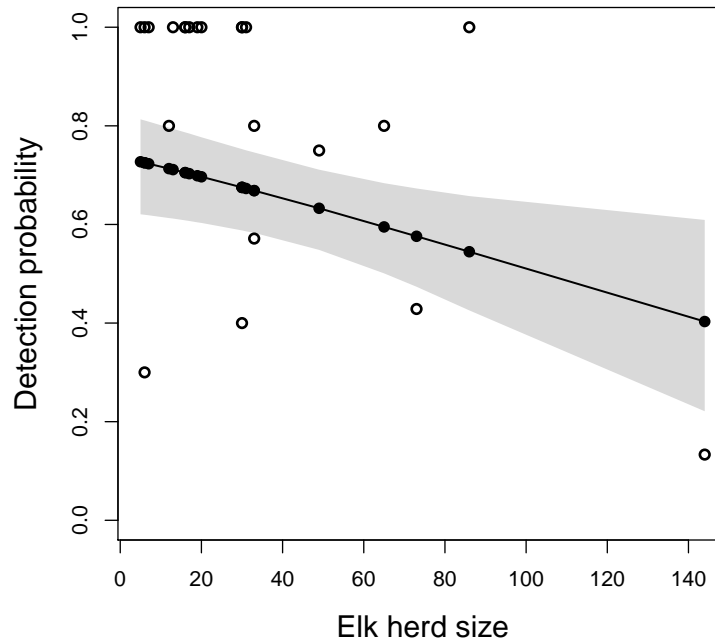


Figure 2.5: The probability of detecting collars within a group decreased with group size, with median estimates of fitted values of the detection probability (closed circles) and 95% Bayesian credible intervals of fitted values (shaded gray). The observed proportions of the number of collars detected (open circles) show the high variability in sightability, and that collars are observed more accurately within smaller groups.

Table 2.4: Summary statistics of the posterior distributions of the average overwinter population sizes (μ_{VAL}) of elk in Rocky Mountain National Park and Estes Park for 2011 to 2015 using multiple models, including the open population Lincoln-Peterson style model described above (LP-move), the Dail-Madsen model (DM), the model similar to Pollock’s robust design (Robust), and the Jolly-Seber model (JS). The right two columns represent the equal-tailed Bayesian 95% credible intervals

Models	Year	Mean	Median	SD	X0.025	X0.975
LP-move	2011	544	543	16.94	511	577
	2012	488	488	13.50	462	515
	2013	729	729	29.01	674	788
	2014	827	825	43.71	747	918
	2015	623	619	32.17	573	702
DM	2011	9049	9045	266.19	8544	9584
	2012	9223	9218	255.37	8740	9735
	2013	8477	8472	249.63	8007	8978
	2014	8842	8837	249.48	8371	9343
	2015	8599	8594	251.92	8124	9105
Robust	2011	1378	1378	20.72	1338	1419
	2012	2832	2832	37.37	2760	2906
	2013	2708	2708	40.09	2631	2788
	2014	3067	3067	39.29	2991	3145
	2015	2741	2741	38.33	2667	2817
JS	2011	79	79	0.93	78	81
	2012	139	139	1.61	137	143
	2013	149	149	1.67	147	153
	2014	140	139	2.34	136	145
	2015	139	139	2.14	135	144

2.3 Discussion

We developed a Bayesian hierarchical model that exploited multiple sources of data to estimate animal abundance when scales of animal movement are greater than the fixed spatial domain of management decisions. We illustrated the use of our approach to obtain the average over-winter population sizes of elk on the winter range of the Estes Valley during five years of surveys (see Figure 2.4 and Table 2.2). We used movement data to improve inference for animal abundance within a fixed study area and used auxiliary detection data to calibrate missed resights. Abundance estimators typically only provide information about the size of a population, however, our model also provided inference for multiple demographic population parameters that can be useful for management.

Movements of animals across management jurisdictions pose challenges for estimating population sizes because the scale of inference often fails to correspond to the scale at which decisions are made. For example, movements can occur on large geographic scales, such as the seasonal migration of elk from the alpine during summer to lower valleys during winter (Hess, 1993). Movements can also occur on small geographic space and time scales, such as movements among the conservation area of RMNP, the nearby town of Estes Park, and the foothills, throughout winter. These smaller scale movements can confound efforts to accurately estimate population sizes because the number of individuals using the managed areas varies. We explicitly modeled movements with a Markovian process model coupled with a multinomial data model of telemetry location data. Thus, we were able to accurately estimate the number of marked individuals available for sampling during any given survey. The movement probabilities showed a consistent trend; elk were more likely to remain in their location from one week to the next, than to move to other areas. Nevertheless, study area boundary movements were sufficiently occurring to necessitate accounting for these small scale movements in the model.

Median annual survival probabilities during the later years of this study (Table 2.3) resembled those of Brodie et al. (2013), who estimated annual elk survival of 0.95 in elk populations without predators, and 0.94 in elk populations that were not hunted. However, the low survival probability for the first year, 0.87 (BCI=0.76,0.94) is similar to the estimated survival probability in Monello et al. (2014) of 0.85 (BCI=0.75,0.93), with overlapping credible intervals. The low probability of survival is likely due to the fact that all of the elk were captured and collared in RMNP, and a high proportion of collared elk wintered in the park during that year. The increase in annual survival for subsequent years may be due to the inclusion of elk that were captured and collared outside the park, inclusion of elk that wintered in areas other than RMNP, and the greater elk population expanding into new habitat use areas outside the park, where sources of mortality differ and chronic wasting disease prevalence has been found to be lower (B. Kraft, R. Monello, M. Miller, L. Wolfe *unpublished data*).

Elk aggregate into large herds during winter, particularly for calf and cow groups. These large groups can prevent observers from resighting marks, which in turn, can lead to biased overestimates of the population size. We were able to calibrate the resighted marks using auxiliary telemetry data collected during ground census and adjusting for imperfect detection of resights. Ideally, these auxiliary data could be collected throughout the study, but we were only able to collect these observations during a small fraction of ground surveys and then applied the results to all of the surveys across all years. In some cases, we might be overcompensating for missed resights, as reflected in the high probabilities of detection within the N -mixture model during some of the winter survey weeks, which then led to convergence problems in the MCMC samplers. The average population sizes across all winter months were not sensitive to this over-compensation because the estimates borrowed strength from the repeated surveys and hierarchical structure of the model (Hobbs and Hooten, 2015). We obtained population sizes during each month of winter, however, given the convergence diagnostics, we suggest caution interpreting these statistics.

We assumed that the probability of detection was constant among all collared elk, despite the fact that brightly colored collars deployed by Colorado Parks and Wildlife were more readily visible to ground count volunteers than the brown collars deployed by the National Park Service. Additionally, the telemetry data were based on collars deployed only on adult female elk. We applied the estimates of the probability of detection in the abundance estimator to data consisting of all sex and stage classes. This is a realistic assumption for juveniles and yearling males, because juveniles, yearling males, and adult females aggregate into large herds during winter. Adult males form separate groups and typically have lower probabilities of detection. Because adult males comprise a relatively small proportion of the overall population that uses RMNP and EP, assuming a constant probability of detection for all classes is unlikely to have a substantial influence on overall population size predictions.

There was notable variability of the elk population sizes in RMNP throughout the years of study (Figure 2.6). This variation could result from variable snow depth, moisture regimes (there were drought conditions through 2013), forage conditions, development in the town of Estes Park, and increased fenced areas in the park winter range. The estimated number of elk in the Estes Valley, CO was much lower than historical estimates (Lubow et al., 2002), due to several reasons including a population reduction prescribed in the elk and vegetation management plan (National Park Service, 2007) and a subsequent increase in the number of elk that winter outside of the Estes Valley in the foothills. The population of elk in RMNP was lowest during the second season of the study, during the 2012-2013 winter, with the median of the marginal posterior of $\mu_{\text{RMNP}} = 171$ (BCI = 158,187). This estimate was lower than a suggested minimum limit of 200 elk as described by recent ecosystem models developed for the winter range (National Park Service, 2007). Subsequent increases were likely due to a larger number of elk remaining in the Estes Valley and RMNP during winter, versus going to the foothills, rather than resulting from greater survival or recruitment.

Aerial surveys were used to census the elk in RMNP annually from 1994 to 2014. These surveys were expensive, dangerous, and required staff to be constantly available throughout

winter to exploit rare periods of weather suitable for flying. Expense and limited opportunity for flying prevented multiple samples so that during most years, only a single survey was made. Overwinter variability in population size was necessarily ignored during these years. Ground based census methods, consisting of monthly counts throughout winter, permitted estimates of sampling variation. However, ground surveys had their own set of limitations, such as the restriction of observations to occur close to accessible roads, and difficulty in properly training volunteers. The National Park Service repeated samples to minimize the impact of these potential problems. Annual aerial surveys that were corrected using a sightability model (Lubow 2015, *unpublished report*) were similar to the medians of the posterior distributions of population sizes based on the N -mixture model used here (Figure 2.7).

Multiple models showed unrealistic results of the overwinter means of abundance across the years of the study (Table 2.4). The Dail-Madsen model led to posterior means that were unrealistically high, and the Jolly-Seber model led to posterior means that were unrealistically low. Not accounting for temporary emigration, observation error of the telemetry data, and observation error of the resighted marks also led to unrealistically high mean abundance. While population sizes obtained using alternative models and different data are naturally expected to differ, the substantial variability in posterior means was surprising, and shows the difficulty of implementation of ground based methods for surveys of large mobile wildlife species.

Using a Bayesian approach enabled us to address sources of uncertainty in both the ecological processes as well as measurement error. We were able to bring together multiple commonly collected data sources, and account for their corresponding variability. Our approach is particularly useful for supporting estimates of abundance of mobile animals that move in and out of conservation areas.

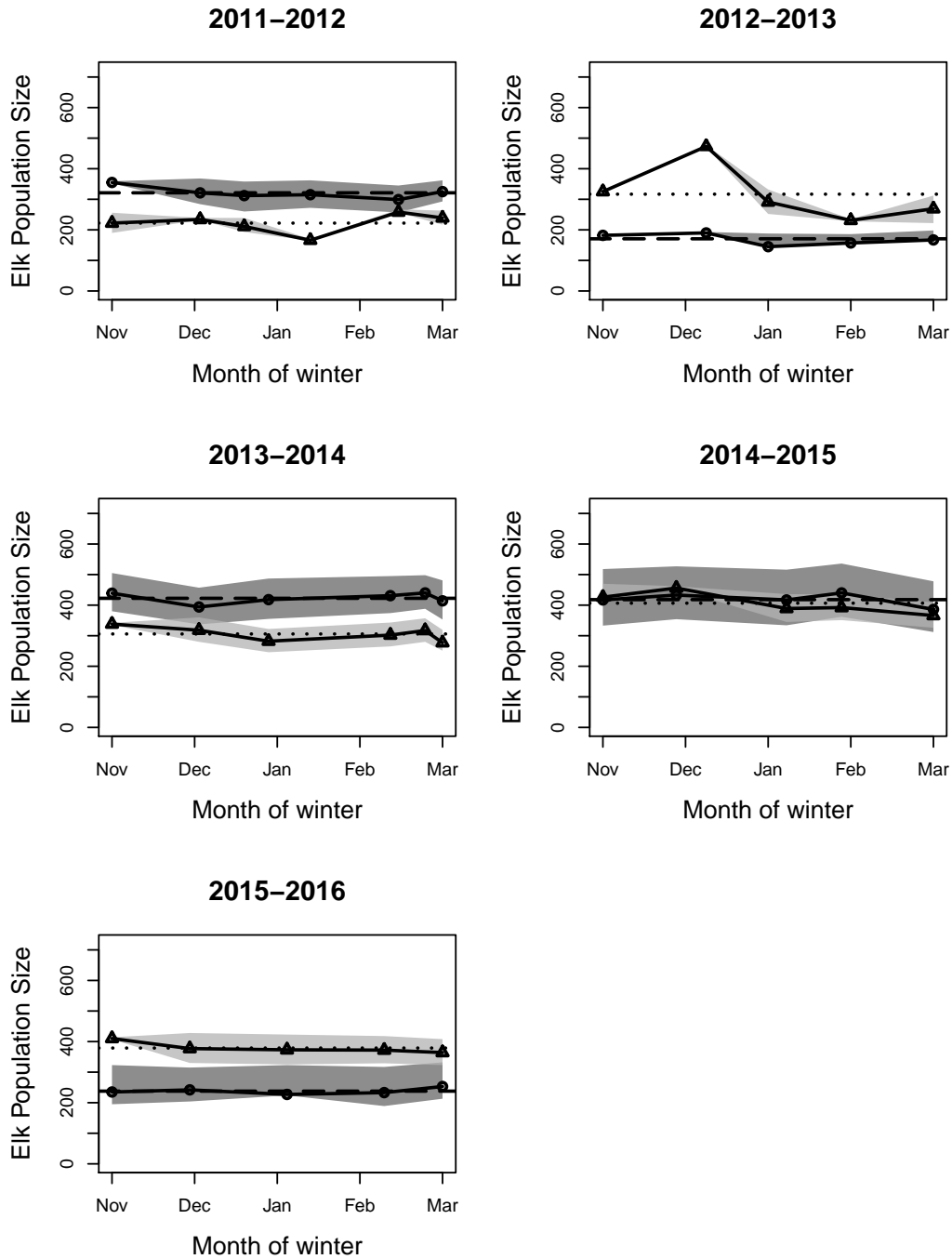


Figure 2.6: The median number of elk using Rocky Mountain National Park throughout winter (circles), and in the town of Estes Park (triangles), shows the population during five seasons. The 95% Bayesian credible intervals for RMNP (dark gray) and EP (light gray) are the shaded regions. The lines with small dashes represent the across winter averages in RMNP, μ_{RMNP} , while the lines with large dashes represent the across winter averages of elk in EP, μ_{EP} .

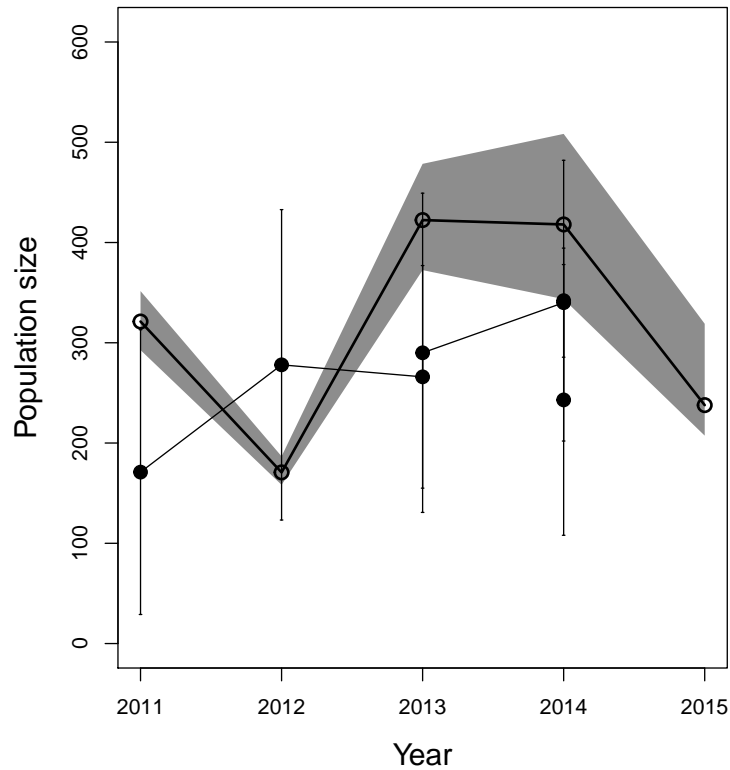


Figure 2.7: Medians of the posterior distributions of the overwinter population sizes in Rocky Mountain National Park (open circles), with equal-tailed Bayesian credible intervals (gray shaded region). Estimated number of elk for each aerial survey based on the sightability model of Lubow et al. (2002) (closed circles). Vertical bars are ± 2 standard errors. No aerial surveys occurred in 2015.

CHAPTER 3

A HIERARCHICAL BAYESIAN NESTED MULTINOMIAL APPROACH FOR HANDLING MISSING CLASSIFICATION DATA ²

Demographic population models use the life cycle of a species to link individual organisms to population dynamics as a whole (Caswell, 2001). These models rely upon classification data to describe the sex, age, or stages of individuals within the population (Caswell, 2001). However, uncertainty associated with these data can alter the inference of vital rates, such as stage or age survival probabilities in marked populations (Challenger and Schwarz, 2009; Kendall, 2004). Ignoring uncertainty in these models can also alter other demographic statistics such as sex ratios (Bender, 2006), which are important for conservation, monitoring, and wildlife management. Physical characteristics, such as differences in color, size, alternative plumage (Rohwer, 1975), and presence or absence of features such as antlers in ungulates (Smith and McDonald, 2002), etc., are used to differentiate stages or sex categories. Behavioral differences, including sexual segregation (Bowyer, 2004; Gregory et al., 2009) and alternative auditory song patterns (Volodin et al., 2015), are another method used to classify individuals. Models depend upon the assumption of perfectly observed mutually exclusive classifications (Agresti, 2002), which is oftentimes unrealistic.

Many species exhibit classification ambiguity, which means that animals may be counted, but cannot be positively classified. As a result, classification data almost always include a category for counts of unclassified individuals. Handling these unknowns has been demonstrably problematic in surveys of aquatic (Sequeira et al., 2016; Tsai et al., 2015; Cailliet,

²Ketz, A. C., Johnson, T. L., Hooten, M. B., & Hobbs, N. T., A hierarchical Bayesian nested multinomial approach for handling missing classification data

2015), terrestrial (Boulanger et al., 2011; White et al., 2001), and aerial (Nadal et al., 2016; Cunningham et al., 2016) species. Classification uncertainty has multiple causes, including physical and behavioral ambiguities, observer skill level, and sampling effort (time). Volunteer participants in ecological surveys are used with increasing frequency (Silvertown, 2009). The skill level of an observer can be difficult, if not impossible to assess, mostly because numerous factors can influence observational ability including environmental variability such as weather, methodological variability such as using scopes or the naked eye, and even the behavior of the surveyed individuals or groups themselves can alter the reliability of classification data. These uncertainties can be mitigated by using only skilled observers or by specialized training, however, even experts can be unable to completely classify observed individuals (Conn et al., 2013; Smith and McDonald, 2002).

Conn et al. (2013) describe three general types of observation problems for classification data, including misclassification, partial observation, or both. In the case of partial observation, individuals are only assigned a category when the observers are certain and the remainder are assigned to an ‘unknown’ category. Partial observations are a form of missing data and can lead to bias for stages or ages of a single species when the age distribution in wildlife populations are not known (Conn and Diefenbach, 2007).

The three types of missing data patterns include missing completely at random (MCAR), missing at random (MAR), and missing not at random (MNAR) (Little and Rubin, 2002). Inference depends upon the missing data mechanism, and how it is accounted for in the model (Nakagawa and Freckleton, 2008). If the data are missing completely at random, the missing data mechanism has no influence on the outcome of the observations, and can therefore be ignored (Little and Rubin, 2002). In ecological studies, the distribution of individuals within a population frequently do not arise from strictly random circumstances even if stochasticity is present. Treating the data that arise from observations of these systems as completely random leads to spurious inference of population trends.

There are several approaches for handling missing data, including ignoring the missing data, data augmentation, and data imputation (Nakagawa and Freckleton, 2008). Bayesian models for missing data in a multinomial framework (Agresti and Hitchcock, 2005) have been used extensively in social and health sciences for dealing with non-ignorable nonresponse data in which individuals may omit answers to some questions or drop out of the study altogether (Kadane, 1985; Nandram and Choi, 2010). These existing methods rely on auxiliary data, such as answers to questions in surveys before drop-out, that can be used as covariates to account for the missing data. However, in ecology, these data are not necessarily available or relevant, necessitating an alternative approach. In this work, we developed multiple approaches for handling partially classified data, in which observers recorded unknowns when they were unsure of the category of individuals.

We use the multinomial distribution to model classification counts and alter the model structure to account for the partial observations by incorporating the missing data mechanism into the model structure. Weak identifiability of the parameters is a fundamental problem for the multinomial distribution and is amplified by flat priors used for the proportions of each level, as is common practice when using the conjugate Dirichlet distribution (Swartz et al., 2004). Introducing additional parameters to account for the non-ignorable partial observations can exacerbate these identifiability problems, therefore, auxiliary data should be used when possible (Conn and Diefenbach, 2007). We developed two approaches for handling partially observed MNAR data when auxiliary data are not available, by explicitly modeling how the missing data observation process is influencing the observation process. We urge ecologists to incorporate their knowledge of the system into models (Hobbs and Hooten, 2015), even if auxiliary data are unavailable or difficult to obtain, to account for the species or stages that are observed and not classified because of uncertainty.

We used a simulation to demonstrate the bias that occurred when the missing data mechanism was ignored for partial observations and how this influenced standard metrics of wildlife populations including demographic ratios (Skalski et al., 2005). Fully observed clas-

sifications of ungulates can be particularly difficult to obtain because physical characteristics of the stages of females can be hard to distinguish. We used the models developed here to obtain the posterior distributions of the ratios of juveniles to adult and yearling females, and the ratios of adult and yearling males to adult and yearling females for elk (*Cervus elaphis nelsoni*) in Rocky Mountain National Park and Estes Park, CO across five winters.

3.1 Materials and Methods

We provide two approaches for modeling the data that properly accounts for uncertainty arising from the unknown category. Data consisted of counts of individuals in J mutually exclusive categories ($\mathbf{y}_{t,i}$), along with an additional category of unclassified individuals ($z_{t,i}$). The likelihood for the data model of these counts was equivalent for both models, and different auxiliary data approaches were used for handling the unclassified data. In the first model, we used a subset of the classification data from a year of the study to inform the distribution of un-classifieds the following year. In the second model, we used a small subset of the classifieds to inform the distribution of the un-classifieds within the same year and excluded that subset from the original classification data.

The classification counts were modeled with a multinomial distribution assuming constant proportions of each category across $i = 1, \dots, I_t$ surveys within $t = 1, \dots, T$ years, such that

$$\begin{pmatrix} \mathbf{y} \\ z \end{pmatrix}_{t,i} \sim \text{multinomial}(N_{t,i}, \mathbf{p}_t) \quad (20)$$

where $N_{t,i} = \sum_{j=1}^J y_{t,i,j} + z_{t,i}$. The vector of proportions (\mathbf{p}_t) includes both the proportions for the $j = 1, \dots, J$ classes ($\boldsymbol{\pi}_t$) and the proportion of the unclassified individuals, $p_{z,t}$. The unclassified counts ($z_{t,i}$) were modeled with a nested multinomial with proportions ($\boldsymbol{\omega}_t$) describing the J classes and the constraint $\sum_{j=1}^J \omega_{j,t} = 1$. Observed proportions for each

category when $J = 4$ are

$$\mathbf{p}_t = \begin{pmatrix} \pi_{1,t} - \omega_{1,t} \times p_{z,t} \\ \pi_{2,t} - \omega_{2,t} \times p_{z,t} \\ \pi_{3,t} - \omega_{3,t} \times p_{z,t} \\ \pi_{4,t} - \omega_{4,t} \times p_{z,t} \\ p_{z,t} \end{pmatrix}. \quad (21)$$

A prior Dirichlet was specified using independent gamma distributions (Gelman et al., 2014), with a uniform prior for the unknown category.

$$\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\alpha}_t) \quad (22)$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}^*_t / \alpha_0 \quad (23)$$

$$\alpha_0 = \sum_{j=1}^J \alpha^*_j \quad (24)$$

$$\alpha^*_j \sim \text{gamma}(.001, .001) \quad (25)$$

$$p_{z,t} \sim \text{uniform}(0, 1). \quad (26)$$

Additional data, such as environmental covariates or observations to assess the sampling effort and expertise of observers were not collected in our study system. These data are necessary to avoid identifiability problems for obtaining the posterior distributions of $\boldsymbol{\omega}_t$. Instead, we made two assumptions using knowledge of the species. We assumed the population was distributed in groups and that the composition of the groups depended on the sex/stages of the individuals within those groups.

Sexual segregation is common in vertebrate species (Ruckstuhl and Neuhaus, 2005), particularly for ungulates (Bowyer, 2004), and leads to different compositions of assemblages. Juveniles of both sexes, and yearling and adult females aggregate into large herds during

winter, with the occasional presence of very few yearling and adult males. Conversely, yearling and adult male elk typically form segregated smaller herds during winter or demonstrate solitary behavior (Bowyer, 2004). We assumed that unclassified individuals were likely the result of difficult to distinguish juvenile, yearling and adult female herds.

We defined the subset of the data for the k th group within survey i of the t th year, $(\mathbf{x}_{t,i,k})$, based on the criteria that the sum of the juvenile, yearling and adult female elk was greater than the sum of the yearling and adult male elk ($\sum_{j=1}^2 x_{j,t,i,k} > \sum_{j=3}^4 x_{j,t,i,k}$), and that there were no unclassified observations in these subsetted groups. Although this assumption is highly specific for our study system, our approach is easily altered for other species, particularly because sexual segregation and sexual dimorphism are common (Ruckstuhl and Neuhaus, 2005).

In the first model, we used an empirical Bayesian approach (Deely and Lindley, 1981), where all subsetted classification data from year t ($\mathbf{x}_{t,i,k}$) were used to predict the posterior distribution of the unknowns the following year ($\boldsymbol{\omega}_{t+1}$). For the first year of the study, we defined a prior distribution for $\boldsymbol{\omega}_1$ derived from moment matching proportions (Hobbs and Hooten, 2015) based on the mean proportions from Peek and Lovaas (1968) for a winter range area heavily populated by juveniles and adult female elk groups in Montana. The empirical Bayes model for unclassified data was

$$\mathbf{x}_{t,i,k} \sim \text{multinomial}(\sum_{j=1}^J x_{j,t,i,k}, \boldsymbol{\omega}_{t+1}), \quad (27)$$

$$\boldsymbol{\omega}_1 \sim \text{Dirichlet}(23, 71, 4, 2), \quad (28)$$

$$\boldsymbol{\omega}_{t+1} \sim \text{Dirichlet}(1, 1, 1, 1), \quad (29)$$

for the k th group in the i th survey of the $t = 1, \dots, T - 1$ years.

In the second model, we used an out-of-sample approach where a small random sample of the subsetting auxiliary data, $\mathbf{x}_{t,i,k}^*$, was used to predict the posterior distributions of the proportions of each of the missing data classes $\boldsymbol{\omega}_t$ within that same year. The subsampled data were removed from the overall data, such that $\mathbf{y}_{t,i}^* = \mathbf{y}_{t,i} - \sum_{k=1}^{K_{t,i}} \mathbf{x}_{t,i,k}^*$, ensuring that the data were only used once. Thus, the out-of-sample model was

$$\mathbf{y}_{t,i}^* \sim \text{multinomial}(N_{t,i}^*, \boldsymbol{\pi}_t), \quad (30)$$

where $N_{t,i}^* = \sum_{j=1}^J y_{j,t,i}^* + z_{t,i}$. The nested model for the unclassifieds was

$$\mathbf{x}_{t,i,k}^* \sim \text{multinomial}\left(\sum_{j=1}^J x_{j,t,i,k}^*, \boldsymbol{\omega}_t\right), \quad (31)$$

$$\boldsymbol{\omega}_t \sim \text{Dirichlet}(1, 1, 1, 1). \quad (32)$$

For comparison, we used a third model of the classifications suggesting a missing completely at random process (hereafter, trim model), by ignoring the missing data given by

$$\mathbf{y}_{t,i} \sim \text{multinomial}(N_{t,i}, \boldsymbol{\pi}_t), \quad (33)$$

$$\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\alpha}_t), \quad (34)$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}^*_t / \alpha_0, \quad (35)$$

$$\alpha_0 = \sum_{j=1}^J \alpha_j^*, \quad (36)$$

$$\alpha_j^* \sim \text{gamma}(.001, .001). \quad (37)$$

for $j = 1, \dots, J$ categories, $i = 1, \dots, I_t$ surveys and $t = 1, \dots, T$ years, where $N_{t,i} = \sum_{j=1}^J y_{j,t,i}$.

3.1.1 Model fitting

A simulation was conducted to test the ability of all models to find the posterior distributions of known parameters. The marginal posterior distributions were approximated using Markov chain Monte Carlo (MCMC) using the ‘dclone’ package (Sólymos, 2010) for parallelization of the JAGS software (Plummer, 2014a) in R (R Core Team, 2016). Each of the models were fit separately, using 3 chains consisting of 100,000 MCMC iterations and a burn-in of 25,000 iterations. Standard diagnostics indicated no lack of fit, and Gelman-Rubin diagnostics indicated convergence of all posterior distributions (Gelman et al., 2014). We calculated the difference between the predicted and true proportions of the simulated classes of adult and yearling females because the asymptotic stable stage distribution is most sensitive to variations in adult female survival (Gaillard et al., 2000), and because this proportion is used for estimating demographic ratios (Skalski et al., 2005). For each MCMC iteration, we derived the difference between the predicted values and the true value that was initially used for generating data. The empirical Bayes model and the trim model were approximated with varying values of the proportion of unclassified individuals, $p_z \in \{0.1, \dots, 0.7\}$ to examine the influence of bias when ignoring the proportion of unknowns. We then determined the influence of the out-of-sample size on the width of the equal-tailed Bayesian credible intervals of the proportion of adult and yearling females by repeatedly fitting the out-of-sample model for increasing sample sizes (L) of auxiliary data $\mathbf{x}_{t,i,k}^*$.

Five years of elk classification data were collected during ground transect surveys on the winter range of Rocky Mountain National Park and in the town of Estes Park, Colorado from 2012-2016. Fifteen surveys occurred throughout winter during each year (except twelve surveys the first year) and were executed with volunteer observers. There was substantial variation among volunteers in their ability to classify elk. Smith and McDonald (2002) estimated the average discrepancies of classifications for antler-less elk, consisting of juveniles,

yearling and adult females to be 14%, even for skilled observers, demonstrating the difficulty of obtaining complete classification observations.

The posterior distributions of the proportions of elk in the four sex/stage classifications across five years were approximated using all three models (empirical Bayes, out-of-sample, and trim). We calculated the posterior distributions of the derived ratios of juveniles to adult and yearling females, as well as the ratios of adult males to adult and yearling females. For the out-of-sample model, we used a sample of 8 observations of the $\mathbf{x}_{t,i,k}$ within each year to approximate the posterior distributions of ω_t . The posterior distributions of each of the models were approximated using 3 chains consisting of 100,000 MCMC iterations. Gelman-Rubin diagnostics indicated convergence of all posterior distributions (Gelman et al., 2014).

3.2 Results

Simulation results indicated that an increasing proportion of unclassified individuals (p_z) amplified the bias of the proportion of yearling and adult females (Figure 3.1 A) when unknowns were ignored. Derived from $\pi_{2,t}$, both of the ratios of juveniles and adult males to adult and yearling females were overestimated (Figures 3.1 B and C). The equal tailed 95% Bayesian credible interval width decreased as the out-of-sample size increased, until approximately 8-10 samples, after which very little change occurred for the credible interval width (Figure 3.2).

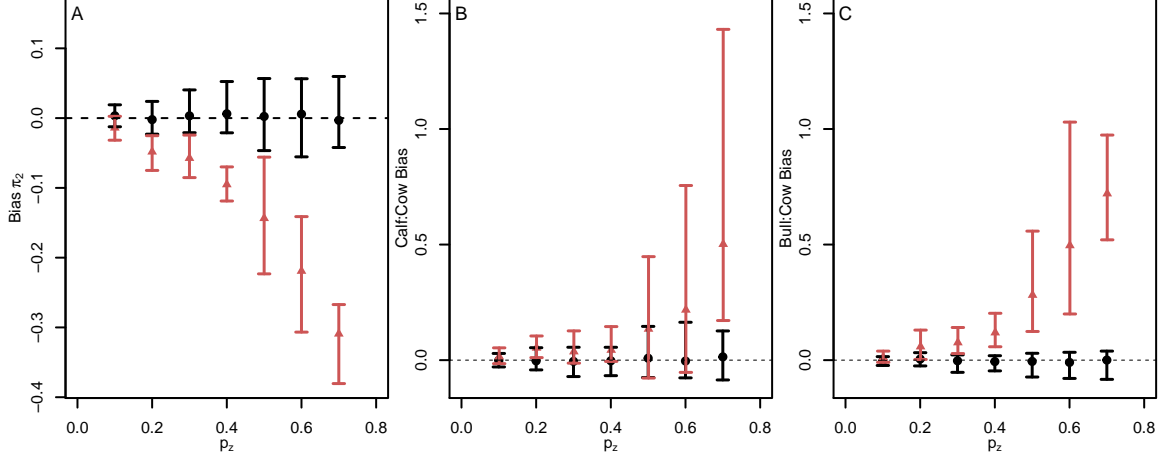


Figure 3.1: (A) The posterior distributions of the difference between the generated proportion of π_2 and the true value for the empirical Bayes approach (black circles), and ignoring the unclassified data (red triangles), for increasing proportions of missing unclassified data. The vertical bars represent the 95% equal-tailed Bayesian credible intervals. The horizontal dashed line indicates no bias. (B) The increasing bias for the juvenile to adult and yearling female ratios, and (C) the increasing bias for the ratios of adult and yearling males to adult and yearling females, as the proportion of unknowns increases.

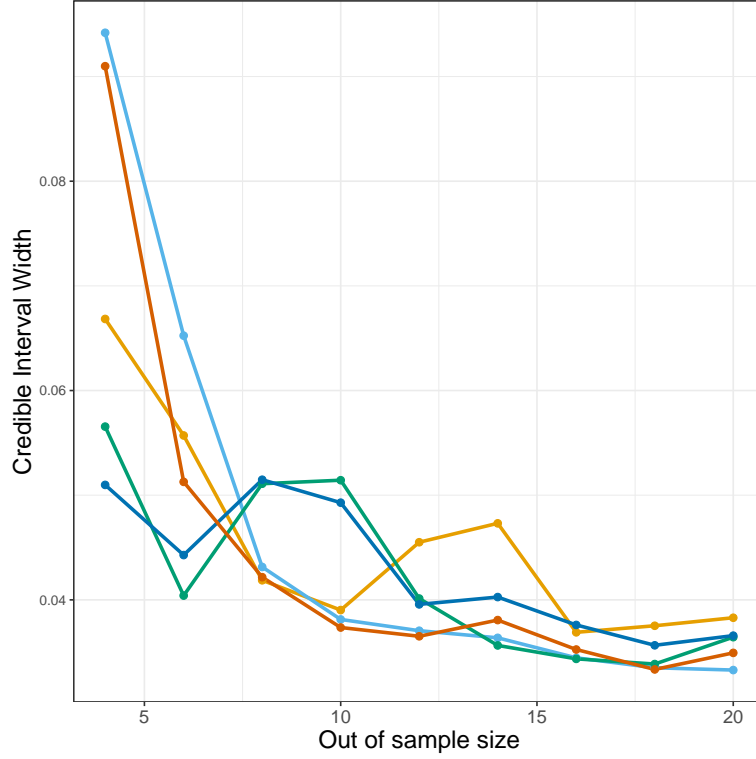


Figure 3.2: The equal-tailed 95% Bayesian credible interval width of the proportion of adult and yearling females (π_2) in the simulation, for year 1 (orange), year 2 (light blue), year 3 (green), year 4 (dark blue), and year 5 (red) decreased as the size of the out-of-sample subset of data increased.

The medians of the marginal posterior distributions of the proportion of adult and yearling females for elk in Rocky Mountain National Park, were similar for the empirical Bayes and out-of-sample models, although differed substantially from the trim model (see Tables 3.1, 5.3, 5.4, 5.5). The empirical Bayes and out-of-sample models had nearly completely overlapping marginal posterior distributions of the ratios of juveniles to adult and yearling females throughout the years (Figure 3.3 A) and for the ratio of adult males to adult and yearling females (Figure 3.3 B). The posterior distributions for both ratios under both proposed models were substantially different from the posterior distributions of the trim model.

The posterior distributions for the proportions of adult and yearling females (π_2) and proportions of adult males (π_4) across all years of the study demonstrated the altered infer-

ence that occurred when the partial observations were accounted for in the model (Figure 3.4). For three of the years, the posterior distributions of the proportion of adult males were nearly identical for the empirical Bayes and out-of-sample models, but with no overlap of the trim model, suggesting that the bias that occurs when ignoring the unclassified data greatly alters inference.

Table 3.1: Medians of the posterior distributions of the proportion of each of the classes (π_t) from 2012 through 2016 for elk in Rocky Mountain National Park derived from the three models including the empirical Bayes approach (EBA), out-of-sample (OOS), and ignoring (Trim) approaches.

Year	Parameter	EBA Median	OOS Median	Trim Median
2012	π_1	0.148	0.152	0.148
	π_2	0.534	0.561	0.546
	π_3	0.095	0.065	0.066
	π_4	0.223	0.222	0.239
2013	π_1	0.181	0.183	0.182
	π_2	0.616	0.615	0.526
	π_3	0.066	0.054	0.063
	π_4	0.138	0.147	0.228
2014	π_1	0.179	0.188	0.183
	π_2	0.595	0.576	0.519
	π_3	0.073	0.078	0.084
	π_4	0.153	0.158	0.214
2015	π_1	0.159	0.153	0.153
	π_2	0.592	0.597	0.560
	π_3	0.063	0.055	0.065
	π_4	0.186	0.194	0.222
2016	π_1	0.201	0.203	0.202
	π_2	0.587	0.577	0.577
	π_3	0.066	0.068	0.067
	π_4	0.146	0.151	0.153

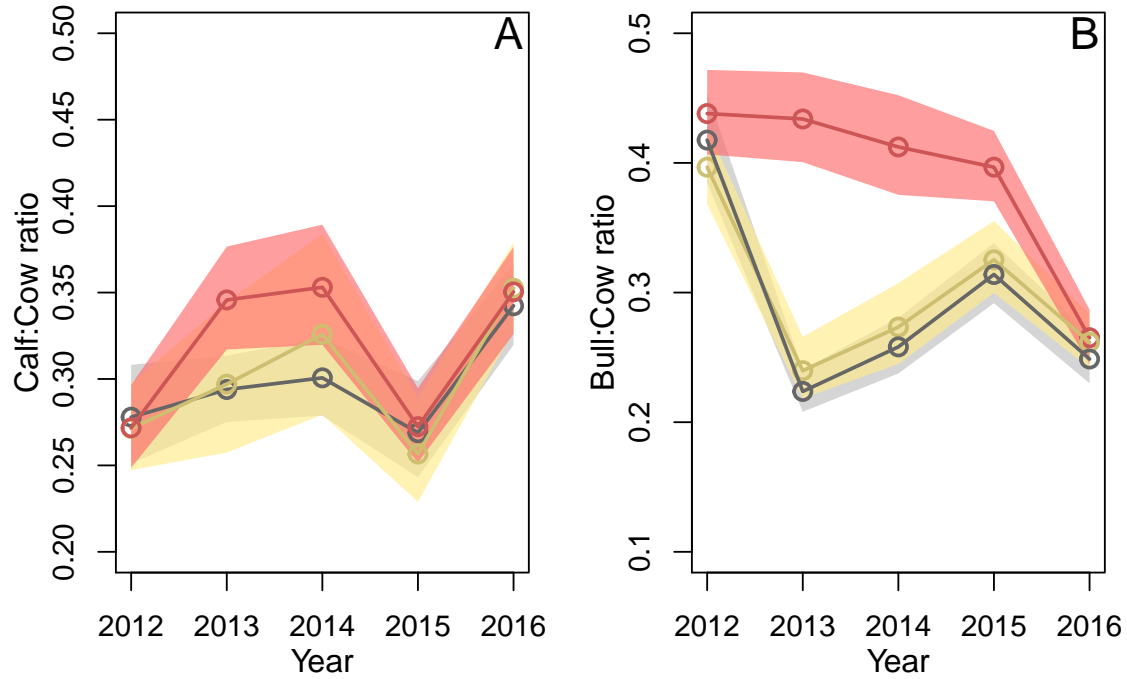


Figure 3.3: The marginal posterior distributions for (A) the ratio of juveniles to adult and yearling females and (B) the ratio of adult males to adult and yearling females, from 2012 through 2016, using the medians (grey circles) of the empirical Bayes model with equal-tailed 95 % Bayesian credible intervals (grey shaded region), medians of the out-of-sample model (yellow circles) and Bayesian credible intervals (yellow shaded region), and medians of the trim model (red circles) and Bayesian credible intervals (red shaded region).

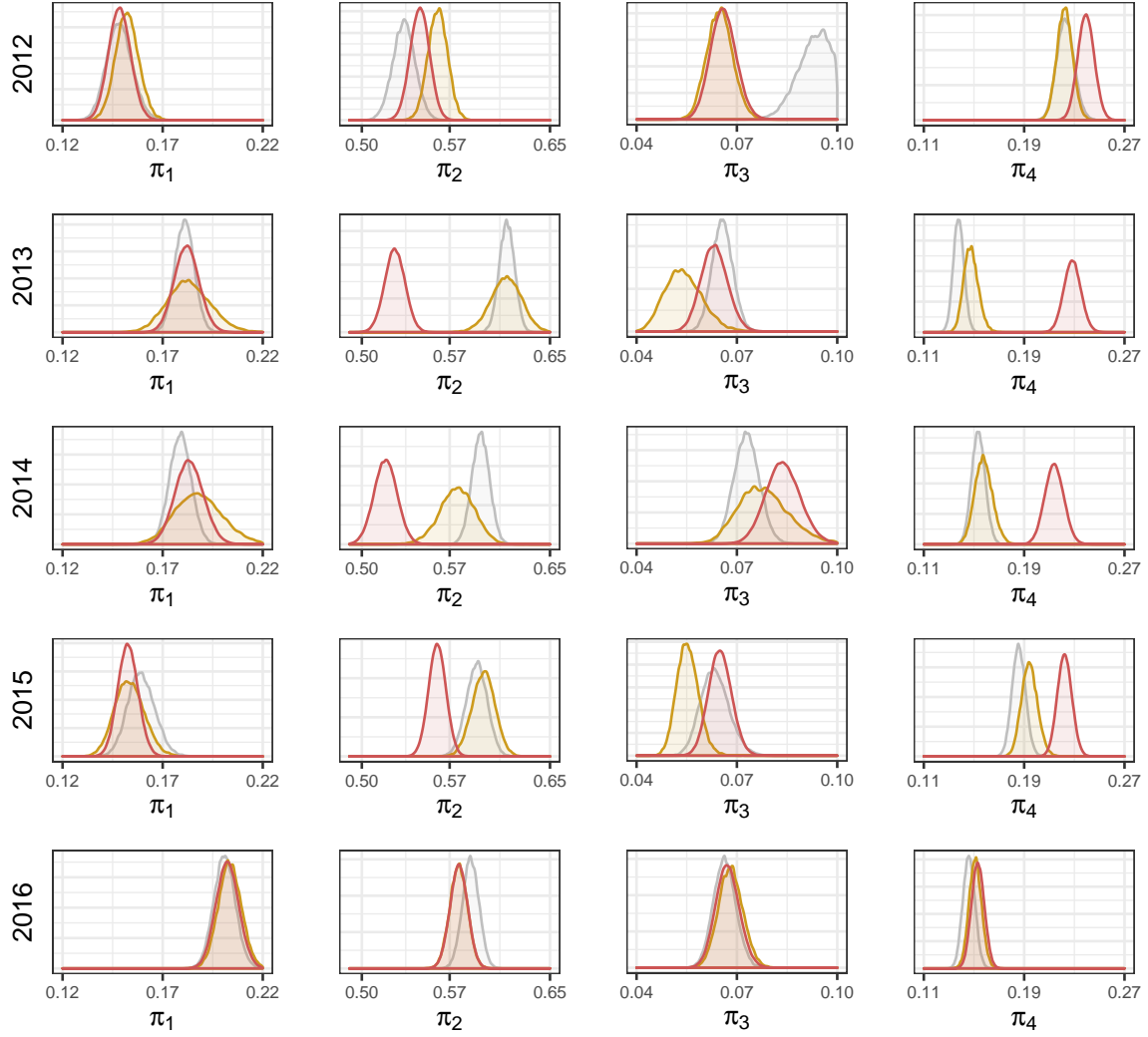


Figure 3.4: The densities of the marginal posterior distributions for the proportions of each stage/sex classes including juveniles (π_1), adult and yearling females (π_2), yearling males (π_3), and adult males (π_4) from 2012 through 2016, using the empirical Bayesian approach (grey), out of sample approach (yellow), and the trim model ignoring the unclassified data (red).

3.3 Discussion

Demographic and population models routinely use classification data for model fitting (Skalski et al., 2005; Caswell, 2001). Uncertainty in classification data commonly arises because individuals are counted but not classified, producing an “unknown” category. Correcting for bias that can result from falsely assuming that this unknown category is proportionally the same as the knowns is critical if these data are to be used for fitting demographic models (Conn et al., 2013).

There are three problems with classification data, including misclassification, partial observations, or both (Conn et al., 2013). When classification counts are partially observed, these data are likely to be missing not at random (Little and Rubin, 2002) because most species are not distributed completely randomly. This is notable for ungulates because they aggregate by sex (Bowyer, 2004). We developed multiple approaches for handling partially classified data, in which surveyors recorded unknowns when they were unsure of the sex or stage category of observed individuals.

We used a simulation to demonstrate the increasing sample bias that occurred as the number of unknown individuals increased when these observations were ignored (Figure 3.1). The result is intuitive, but would not have occurred if the data had been missing completely at random. As the out-of-sample size increased, there was no effect on the bias when the proportion of partially observed groups remained constant (Figure 3.5). We showed that the proportion of adult females was underestimated when unknowns were ignored (Figure 3.1). In turn, this led to overestimation of sex and stage ratios.

We used the simulation to determine the number of samples required for an out-of-sample approach, where a small subset of observations were used to estimate the proportions of the unknown counts (Figure 3.2). Calculating the minimum sample size for a multinomial model depends on several factors, including the number of categories and the values of the proportions of each of the categories (Thompson, 1987). For this reason, we advise the use

of simulation for determining the minimum sample size to use as much data as possible for the data likelihood. Results suggested that in our study system, after approximately 8-10 observed groups (Figure 3.2), the width of the Bayesian credible interval no longer decreased substantially. We chose to use an out-of-sample size of 8, to use the greatest possible proportion of the data in the likelihood.

Simulations showed that the empirical Bayes model provided the most accurate bias adjustment for the posterior distributions of the proportion of adult and yearling females (Figure 3.6). The out-of-sample model was able to recover parameters, but the credible intervals of the marginal posterior distributions of adult and yearling females proportions were less centered around the true parameter values, although many of the equal-tailed 95% Bayesian credible intervals were able to capture them.

The results of our case study showed little difference in the posterior distributions for the empirical Bayes and out-of-sample models, but the proportions of adults of both sexes were substantially different from the trim model (Figure 3.4). This suggests that there may be no difference among years for the distribution of juvenile, yearling and adult female groups, which calls into question the assumption of a time-varying composition explicit in the empirical Bayes model. However, it could also mean that both models adequately adjust for the bias resulting from ignoring partial classifications.

We made the critical assumption that the unclassified data arose from groups of juveniles and adult females because adult and yearling males can be easily differentiated based on their antlers (Smith and McDonald, 2002). Although this particular assumption is highly specific for elk, there are numerous examples of other species where ecologists could apply similar knowledge of the biology of the species, in order to subset the data for estimating the proportions in the nested multinomial models that we developed. For example, bighorn sheep (*Ovis canadensis*) in Colorado provide an identical classification problem to elk, because juvenile, yearling, and adult females aggregate and are difficult to differentiate (George et al., 2009). A different system for which our models could be useful is for biannual surveys of

white-tailed ptarmigan. Classifications only occur for spring surveys when all individuals are physically captured and sex/stage status can be accurately determined (Wann et al., 2014). During fall surveys, approximately 20% of observed individuals cannot be classified because the ptarmigan have not yet molted, so identification of sex is impossible for these individuals (Wann et al., 2014). Because hunting licenses are deployed in the fall, it would be useful for managers to have an accurate post breeding fall estimate of sex and juvenile ratios (Soininen et al., 2016). Thus, we could use the classification data from the spring surveys to determine the unclassified ptarmigan distribution in autumn.

The two proposed models that account for missing data have strengths and weaknesses that could be exploited for different study systems. Empirical Bayesian methods are typically criticized for using the data twice and for assuming exchangeability (Gelman, 2008). However, for rare or difficult to detect species, empirical Bayes would be a better choice than the out-of-sample model because all of the data collected are used in the data observation likelihood. For species that are neither rare nor difficult to detect, such as caribou (Boulanger et al., 2011), the out-of-sample model avoids using the data twice with little loss of information.

One of the fundamental assumptions of the multinomial distribution is that the outcomes of each event are mutually exclusive and all inclusive (Agresti, 2002). In this paper, we developed a nested multinomial distribution to account for circumstances when this assumption is violated. We used multiple approaches that overcame this assumption and improved inference. Another assumption of the multinomial model is that detection is constant for all class proportions (Skalski et al., 2005). Elk sexually segregate (Bowyer, 2004; Gregory et al., 2009) and consequently, it is unlikely that detection is constant or equivalent for all classes. We explicitly rely upon their aggregating behavior to adjust the marginal posterior distributions of the proportions of each of the classes.

Conn and Diefenbach (2007) provided a general statistical framework for estimating the stage distribution of a sample when mis-classification rates could be estimated, which occurs in a population with known ages or if double observer sampling protocols are followed (Conn

et al., 2013). We build upon this work for modeling wildlife populations in which classification data need analysis and auxiliary data are unavailable or difficult to obtain. Identifiability problems arise (Swartz et al., 2004), but these can be mitigated by using informed priors and incorporating biological knowledge of the study system.

We presented our models in a generalized framework so that they could be altered for other systems. It is essential for these models to have auxiliary data, or at the very least, auxiliary information that can be used to obtain the distribution of unknown partially classified data for the parameters to be identifiable. We improved the inference of the proportions of four sex/stage classes ($\boldsymbol{\pi}_{t,i}$) of elk on the winter range of Rocky Mountain National Park and Estes Park, CO (Figure 3.4), and in turn, we were able to improve inference for demographic ratios used by wildlife managers.

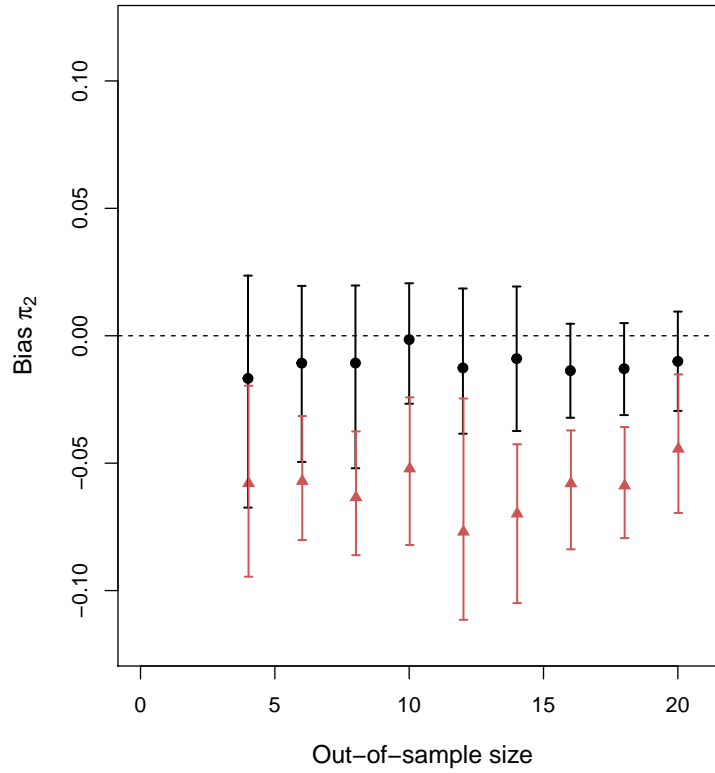


Figure 3.5: The posterior distributions of the difference between the generated proportion of π_2 and the true value for the out-of-sample approach (black circles), and ignoring the unclassified data (red triangles), for a constant proportion of missing unclassified data, with increasing the sample sizes used to estimate the distributions of unknowns. The vertical bars represent the 95% equal-tailed Bayesian credible intervals. The horizontal dashed line indicates no bias.

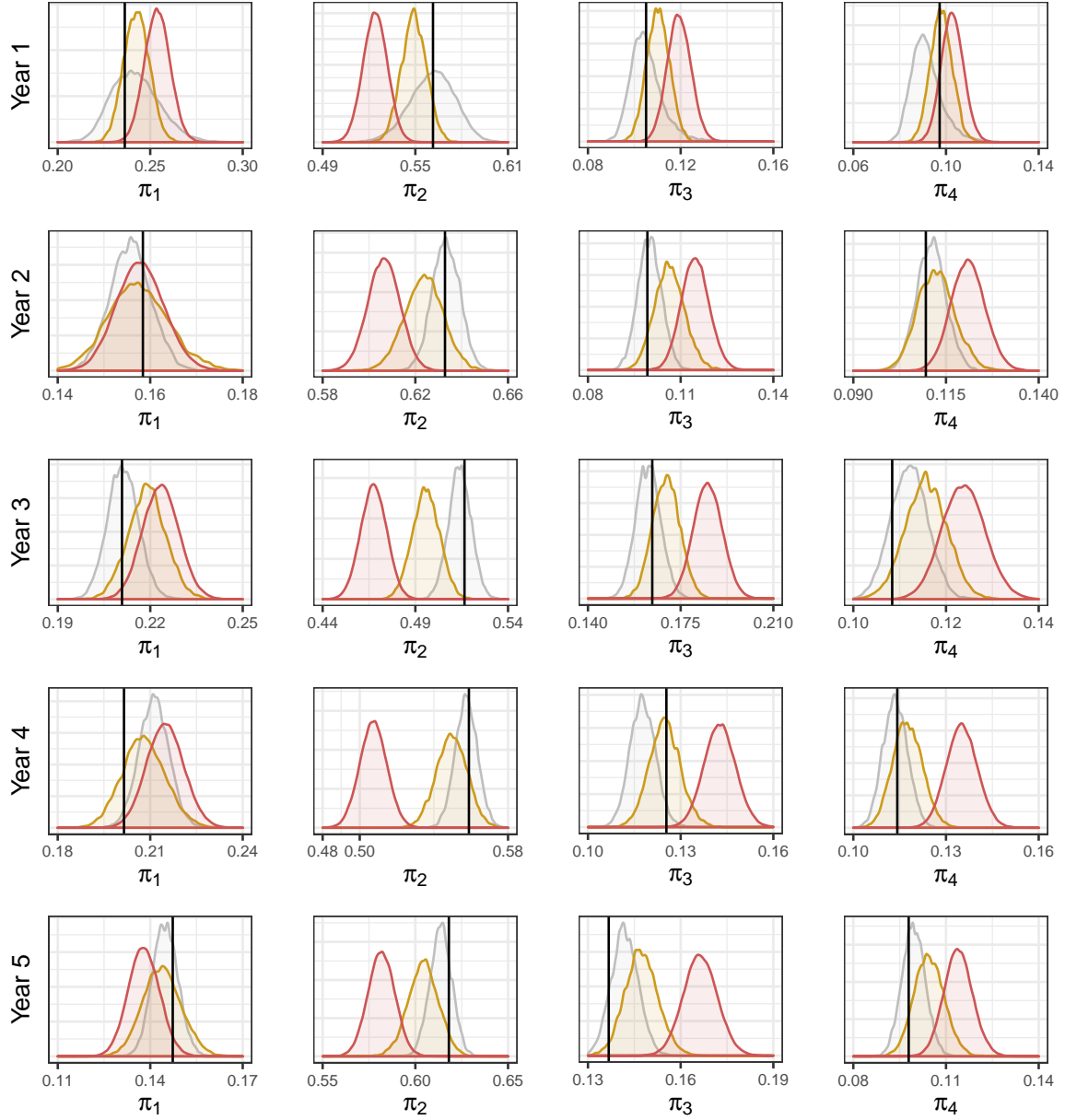


Figure 3.6: The densities of the marginal posterior distributions for the proportions of each simulated stage/sex classes including juveniles (π_1), adult and yearling females (π_2), yearling males (π_3), and adult males (π_4) for all five years of the simulation, using the empirical Bayesian approach (grey), out of sample approach (yellow), and the trim model ignoring the unclassified data (red). The vertical black line is the true value of the parameter used to generate the data.

CHAPTER 4

INFORMING MANAGEMENT WITH MONITORING DATA: THE VALUE OF BAYESIAN FORECASTING ³

The fundamental challenge of resource management is to evaluate the ability of alternative actions to meet goals for the future. This statement holds true for privately and publicly owned resources and for all classes of institutions that manage those resources – governments, businesses, and non-profit organizations. Informed management requires three intersecting elements: reliable information on the past and current state of the system being managed, clearly stated goals, and a way to evaluate the effect of potential actions on the future state of the system relative to those goals.

A primary motivation for inventory and monitoring of resources within the U.S. national parks is to provide scientifically reliable information needed to support wise management. Hundreds of different variables are monitored annually based on statistically credible sampling designs in parks nationwide. The mission statement for the National Park Service guides development of goals that are specific to individual parks; goals that are often formulated in conjunction with other management agencies, citizen stakeholders, and local governments. There are usually multiple alternative approaches that could potentially be implemented to move toward achieving those goals, including the null model, “No action.” Thus, many national parks have two of the elements needed for scientifically informed management: information on the current and past state of parks and well-articulated goals for

³Ketz, A. C., Johnson, T. L., Monello, R. J., & Hobbs, N. T. (2016). Informing management with monitoring data: the value of Bayesian forecasting. *Ecosphere*, **7**(11).

the future. However, the third element, an ability to understand the effect of current actions on the future state of parks relative to goals, remains undeveloped.

In this paper, we develop the idea that forecasting models are critical for supporting this third element needed for scientifically informed management of national parks and, arguably, for all natural resources. We use the term forecasting to mean predictions of the future state of a system accompanied by honest estimates of uncertainty (Clark et al., 2001). We develop a framework for forecasting that evaluates actions relative to management goals in national parks. We then illustrate the application of that framework to management of elk and vegetation in Rocky Mountain National Park (RMNP) where elk were overabundant and highly concentrated for decades as a result of anthropogenic ecosystem impacts, leading to deterioration of habitat that supports a wide variety of plants and animals (Schweiger et al., 2016). Elk that use the park are part of a regional population that ranges across park boundaries, necessitating interagency collaboration to coordinate management actions.

4.0.1 A Bayesian approach to adaptive management based on monitoring data

Adaptive management combines science and policy to quantify the outcomes of natural resource management actions in an iterative process of improvement (Holling, 1978; Walters, 1986; Ringold et al., 1996; Nyberg, 1998; Schreiber et al., 2004). The data provided by inventory and monitoring can be combined with management goals within a hierarchical model to make probabilistic forecasts. The reliability of these forecasts, in turn can be evaluated with future data as they become available (Dorazio and Johnson, 2003).

A critical step in adaptive management is specifying a model that reflects what is uncertain about the system and suggests the best course of action given those uncertainties (Walters, 1986; Dorazio and Johnson, 2003). Quantitative models within the adaptive management framework are explicit about assumptions, both in terms of our goals for how a park system should be managed (Rumpff et al., 2011) and our assumptions of how the underlying ecological process works (Restif et al., 2012). Managers can use the inference and support

of these explicit assumptions and structures for guiding their decision making (Restif et al., 2012).

Bayesian modeling offers a natural framework for synthesis of data in support of decision making (Nichols et al., 1995; Dorazio and Johnson, 2003; Hobbs et al., 2015; Raiho et al., 2015). Here, we illustrate the utility of Bayesian hierarchical models for supporting decisions informed by monitoring data, which we define as data collected at regular intervals over an extended period. The approach we describe was originally formulated by Berliner (1996) and has been elaborated by Clark (2003), Cressie et al. (2009), and Hobbs and Hooten (2015).

Bayesian forecasts are predictions of the future behavior of a system that include rigorous estimates of uncertainty. It is reasonable to ask, “Why are forecasting models important? What do they have to do with data and decisions based on data?” The answer to these legitimate questions arises from our original description of the challenge of management, which is “to evaluate alternatives for action in terms of their ability to meet goals for the future.” Data alone cannot inform wise decisions on actions, a truth that is revealed daily in raw numbers cascading from the stock market. Data contain noise as well as information and it is ill-advised to make decisions based on noise. Distinguishing between noise and information in data is the purpose of statistical models. However, the ability of actions to meet goals for the *future* requires a particular type of statistical model, a model capable of making forecasts. Forecasts, we reemphasize, include uncertainty that may arise from many sources. Although many kinds of statistical and mathematical models have been used to make predictions to support management in the past, true forecasting is relatively new.

Goals for management of national parks are often stated in terms of thresholds. In some cases, the goal is to move a state below a threshold, a goal that would be appropriate for the prevalence of some diseases, the abundance of an exotic species, or a measure of noise or light pollution. In other cases, the goal is to move the state above a threshold, which would describe the outcome sought for a threatened, native species or the linear distance of trails in good condition. In all cases, the goal is to maintain the resource within acceptable

boundaries, and alternative actions can be used to move the resource toward these explicit goals. Using monitoring data to evaluate alternatives in a way that includes uncertainty has not been possible until recently.

Bayesian forecasting models provide marginal posterior distributions that describe state variables of interest based on past monitoring data from a particular time frame (Figure 4.1). This form of inference is likely to be familiar to anyone who has used traditional, nonhierarchical statistical analysis of time series. In contrast, hierarchical models also provide *predictive process distributions*, which are simply the probability distributions of future states based on what we have learned from their behavior in the past (Figure 4.1). Modern weather forecasts as well as predictions of voting in presidential elections are based on these distributions.

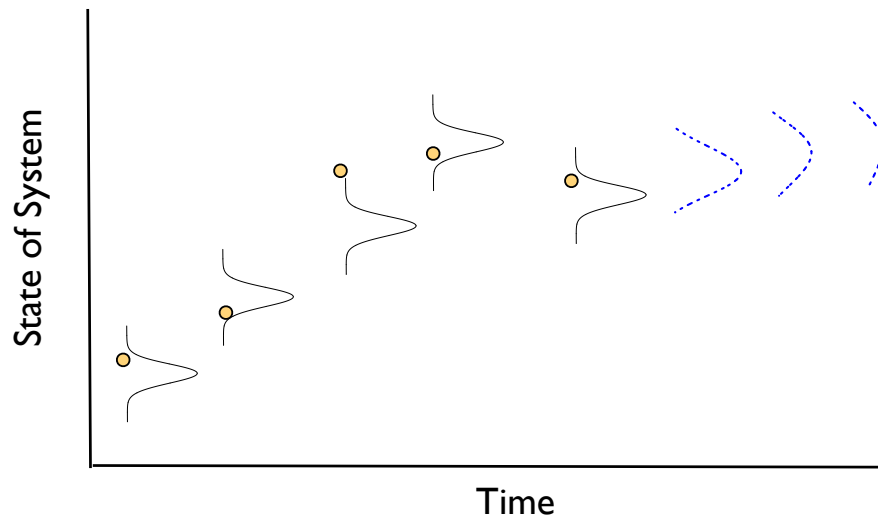


Figure 4.1: Observed data over time are represented by points. The marginal posterior distributions for summary statistics (black lines) show a shift in the system state over time. The marginal predictive process distributions (dashed lines) demonstrate the increasing uncertainty as forecasts are made further into the future.

Predictive process distributions can be related to goals by overlaying one of the thresholds described above (Figure 4.2). For expository purposes, presume that our goal is to move a state below a threshold. Given the uncertainty in the monitoring data and the model, there is some probability that the goal will be reached in the future given *no action*, as shown in the grey shaded area of Figure 4.2. A model portraying the operation of an ecological process (Appendix 5.3.1, Eq. 64) informed by the data and prior information, predicts how the posterior process distribution shifts in response to a “take action” alternative (the solid line in Figure 4.2), increasing the probability of meeting the goal (hatched area) if the action has the desired effect on the future state. The net effect of active management is given by the ratio of the probabilities of meeting the goal by taking the action relative to no action. This analysis supports statistically rigorous statements like “The probability of meeting the goal three years into the future is five times more likely using management action A relative to taking no action, and three times more likely than using management action B.”

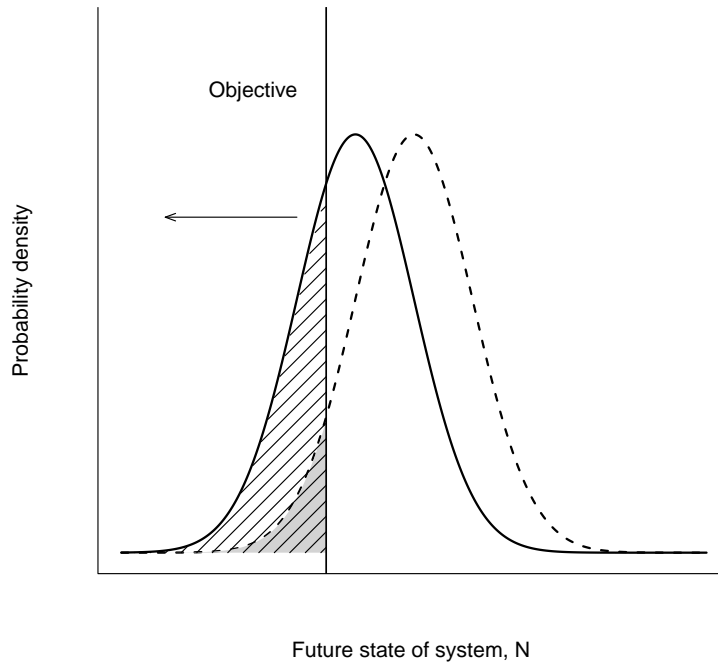


Figure 4.2: Alternatives for management actions can be evaluated by comparing the predictive process distributions relative to a threshold. The dashed line shows the probability distribution of a state variable with no management action at a specified point in the future given no management action. The probability that the population will be below the objective (vertical solid line) is the grey area under the curve. The solid line shows the probability distribution of the state at the same point in the future given management action. The diagonally hashed area under the solid line curve gives the probability of meeting the objective given management action. The net effect of management is the ratio of the hashed and the shaded areas.

4.1 Materials and Methods

4.1.1 Elk in Rocky Mountain National Park

Elk were considered abundant in the Estes Valley when the area was settled by Euro-Americans in the 1860s, but were extirpated by market hunting. Twenty eight elk were translocated from Yellowstone National Park to reestablish a population during 1913-1914, prior to park establishment the following year (Stevens, 1980). Rapid growth of the popula-

tion in the absence of hunting and predation motivated a program of population reduction to improve winter range conditions in the 1940s, which continued until the late 1960s (Hess, 1993).

Population control was replaced by a hands-off approach referred to as natural regulation that allowed elk numbers to increase to ecological carrying capacity after 1968 (Hess, 1993; Sinclair, 1998). Despite hunting that occurred outside the park, the population grew rapidly eventually leading to over-browsing of aspen and willow communities on the elk winter range (Hess, 1993). This initiated a decade of research and development of a management plan that laid out specific population and vegetation goals. This called for using a combination of conservation tools, including population reductions to attain 600-800 elk using the winter range inside RMNP (National Park Service, 2007).

The framework we outline above is general because it is abstract. We now describe a specific example of this adaptive management approach using the elk population in Rocky Mountain National Park as a model system. Long term monitoring of the elk population in RMNP provides the data needed to implement a model capable of forecasting the consequences of alternatives for management. We use a hierarchical model of population dynamics to forecast the consequences of alternative management actions consisting of different culling regimes within the park and different hunter harvest licensing limits outside the park. Other examples of the use of forecasts in a Bayesian framework of adaptive management are described in Horsley et al. (2003), Hobbs et al. (2015), and Raiho et al. (2015).

4.1.2 Monitoring data

The NPS has annually surveyed the elk population in RMNP since 1969 using a variety of methods. Data collected during 1969-1980 were raw counts and classifications from single ground surveys with no attempt to account for detection or sampling variability. The surveys from 1980-1993 were also collected without a robust sampling design using a combination of aerial and ground observations. Single annual aerial counts and classifications during 1994-

2009 were adjusted for imperfect detection with a sightability model to account for elk that were missed because of varying environmental conditions and elk behavior (Lubow et al., 2002). Beginning in 2010, up to three helicopter surveys were attempted annually in order to capture the variability in the number of elk throughout the winter (Schoenecker et al., 2016). However, surveys were sometimes limited to a single flight each year by high costs of flight time, aircraft availability and difficult mountain flying conditions, preventing any way to estimate sampling variability within these years. This motivated development of robust ground survey methods to collect data to account for variation in the use of the park across winter months, while also correcting for sampling error that results from missing elk that are not visible from ground transects.

We used data that were collected during 10 simultaneous ground and aerial surveys that were conducted from 2008 to 2015 to estimate the mean proportion of elk detected in ground surveys (49%) that had been seen during aerial surveys, with an equal tailed Bayesian credible interval (BCI) of (37%,64%). We calibrated all ground surveys across winter using this mean detection probability.

Colorado Parks and Wildlife conducted hunter surveys annually to estimate the number of elk harvested in areas adjacent to the park within the Data Analysis Unit 20. These data were reported without standard errors from 1969 to 1988, and included standard errors from 1989 through the present. Ground classification data of yearling elk were aggregated with adults because the hunter harvest data did not differentiate stage classes older than juveniles.

4.1.3 Process Model

We represented the elk population in RMNP using a discrete, stage structured model (Lefkovitch, 1965; Caswell, 2001) portraying three stage/sex classes: juveniles (n_1), adult females (n_2), and adult males (n_3). Juveniles are both male and female calves under one year of age. Adults are defined as any individuals greater than one year of age. Thus, $\mathbf{n}_t = (n_1, n_2, n_3)'_t$ is the true unobserved stage/sex classified population sizes during the t th

survey year and the total population size is ($N_{\text{total},t} = \sum_{i=1}^3 n_{i,t}$). Model census occurred in February and the birth pulse occurred in June. Let m be the proportion of juveniles that are male, and hence $1 - m$ is the proportion of juveniles that are female. Time varying recruitment parameters (r_t) were defined as the average number of offspring that survive to their first census produced per adult female during year t (Gaillard et al., 1998).

We used a single survival probability for each stage/sex class, where s_1 is the probability that male and female juveniles survive from age 8 months to 20 months, s_2 is the probability of survival of females aged 1.7 years and older, and s_3 is the probability of survival of adult and yearling males over age 1.7 years. We assumed there was no difference in survival of juvenile males and females, which is biologically reasonable because both sexes typically live within the same large herds alongside adult females, at least for their first winter season (Toweill et al., 2002). We define the projection matrix

$$\mathbf{A}_t = \begin{pmatrix} 0 & r_t s_2^{1/3} & 0 \\ (1 - m)s_1 & s_2 & 0 \\ ms_1 & 0 & s_3 \end{pmatrix} \quad (38)$$

that reflects the life cycle diagram in Figure 4.3. The term for recruitment ($a_{1,2}$) has adult survival raised to the 1/3 because females must survive 1/3 of the year between census and the birth pulse (Noon and Sauer, 1992).

The survival parameters reflect mortality caused by predation, environment, and chronic wasting disease (Monello et al., 2014), however, the parameters exclude mortality caused by hunting or culling, which are specified within the process model explicitly. We use hunting data reported by Colorado Parks and Wildlife, defined as $h_{\text{obs},i,t}$ for the i th age and sex class at time t , along with their observed variances $\sigma_{\text{hunt},i,t}^2$. We used the vector $\mathbf{h}_{\text{true},t} = (h_{\text{true},1}, h_{\text{true},2}, h_{\text{true},3})'_t$ to model the unobserved true number of elk removed by hunter harvest

outside the park using:

$$h_{\text{true},i,t} \sim \text{gamma} \left(\frac{h_{\text{obs},i,t}^2}{\sigma_{\text{hunt},i,t}^2}, \frac{h_{\text{obs},i,t}}{\sigma_{\text{hunt},i,t}^2} \right), \quad (39)$$

for $i = \{1, 2, 3\}$. For years prior to 1989, there were no reported observation errors, so a single time and classification invariant model parameter was estimated. Only a proportion of the reported harvest consisted of elk actually removed from the population we are modeling because elk that use RMNP is a subset of the total population subject to harvest outside of the park. This is denoted α_j , for $j = \{1, 2\}$ because the geographic boundary of the hunted area changed in 1989.

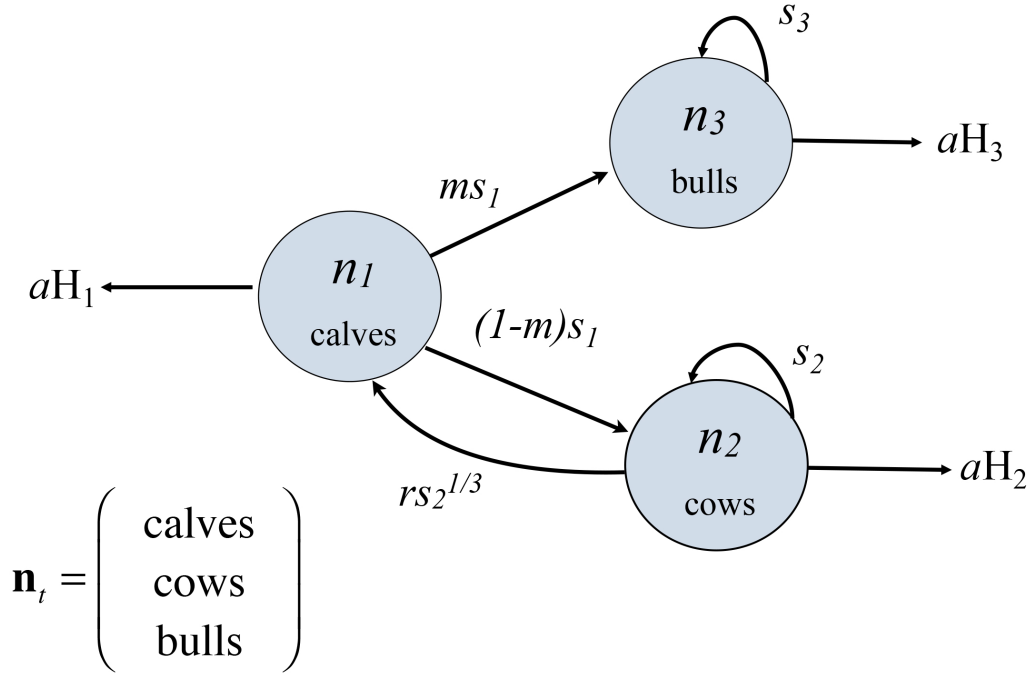


Figure 4.3: The life cycle diagram represents the elk population in three distinct sex and stage classes including juveniles (n_1), adult females (n_2) and adult males (n_3). Parameters in this life cycle include survival (s) and mortality caused by hunting (aH) for each sex/stage class. Additionally, the proportion of juveniles that transition into adult males or females are described by m .

The Elk and Vegetation Management Plan (National Park Service, 2007) requires park managers to determine how many elk, if any, should be culled annually to meet population objectives. Model results were used each year in this decision since 2008. We incorporated culling data into the process model specifying the number of female elk that were culled either before (c_{pre}) or after (c_{post}) the breeding pulse to be the vector $\mathbf{c}_t = (r_t c_{\text{pre}}, c_{\text{post}}, 0, 0)'_t$ where r_t is the average recruitment.

The natural log of the process model can be specified stochastically using a multivariate normal distribution with a vector of means for each stage and sex class ($\boldsymbol{\mu}_t$) such that

$$\boldsymbol{\mu}_t = \log(\mathbf{A}_{t-1} \mathbf{n}_{t-1} - \alpha_j \mathbf{h}_{\text{true},t} - \mathbf{c}_t) \quad (40)$$

$$\log(\mathbf{n}_t) \sim \text{multivariate normal}(\boldsymbol{\mu}_t, \Sigma_p)$$

with a process model covariance assuming independence and variation according to the three classes, defined in log space as a matrix Σ_p with $\sigma_{p,1}$, $\sigma_{p,2}$, and $\sigma_{p,3}$ on the diagonal and 0 elsewhere (see Appendix 5.3.2 for details) ⁴.

4.1.4 Data Model

Data included observations of overwinter population sizes and classification counts from 1969 through 2015. The different sampling regimes over the years required three separate likelihoods to account for uncertainty of the total population sizes. However, the basic structure of the data model was

$$N_{\text{obs},t} \sim \text{normal}(N_{\text{total},t}, \sigma_{\text{obs},t}^2), \quad (41)$$

where $N_{\text{total},t} = \sum_{i=1}^3 n_{i,t}$ is derived from the process model (see Appendix 5.3.3 for additional details on the alternative likelihoods). We justify the choice of the normal distribution for

⁴Inclusion of a briefly used fertility treatment was omitted, but details can be found in Appendix 5.3.3

the data likelihood by the Central Limit Theorem because the \mathbf{N}_{obs} are derived quantities consisting of the overwinter means of counts or derived quantities from multiple counts.

We were also able to link the process model to observations using categorical data consisting of counts within the stage/sex classifications ($\mathbf{y}_{2,t}$). The likelihood of these data is specified with a multinomial distribution such that

$$\mathbf{y}_{2,t} \sim \text{multinomial} \left(\mathbf{p}_t, \sum_{i=1}^3 y_{2,i,t} \right) \quad (42)$$

where $p_{i,t} = \frac{n_{i,t}}{N_{\text{total},t}}$ for $i = 1, \dots, 3$ are calculated from the process model. Observation error arising from the harvest data are described in the previous section. The complete model can be found in Appendix 5.3.2 with the corresponding full posterior and joint distributions. Marginal posterior distributions of all latent quantities and parameters were approximated using Markov chain Monte Carlo (MCMC) methods implemented in the JAGS package (Plummer, 2014b) with R software (Team, 2015). Inference was based on three chains including 100,000 iterations retained after a burn-in of 50,000. Gelman-Rubin diagnostics (Gelman et al., 2014) and visual inspection of trace plots indicated convergence of all chains. Posterior predictive checks using the test statistic $\frac{1}{T-1} \sum_{t=2}^T |y_t - y_{t-1}|$ for time series data (Reilly et al., 2001), did not reveal lack of fit (Gelman et al., 2014). Prior distributions are specified in Table 4.1.

Table 4.1: Prior distributions for model parameters are informed from previous literature on elk vital rates. When literature was unavailable, vague priors were used.

Parameter	Description	Prior	Mean(St.Dev)	Notes
s_1	Juvenile survival	beta(1.51, 2.76)	0.354(0.21)	Raithel et al. (2007)
s_2	Adult female survival	beta(3215.75, 198)	0.942(0.004)	Brodie et al. (2013)
s_3	Adult male survival	beta(31.22, 1.92)	0.942(0.04)	Brodie et al. (2013)
m	Juvenile sex ratio	beta(49.5, 49.5)	0.5(0.05)	Simulation
r_t	Recruitment at time t	beta($g(\mu_r, \sigma_r)$)	μ_r, σ_r	
μ_r	Ave. recruitment	lognormal(log(0.464), 1)	0.464	Raithel et al. (2007)
σ_r	Recruitment st. dev.	uniform(0.001, 0.25)	0.13	simulation
α_1	Proportion hunted	uniform(0, 1)	0.5(0.29)	before/including 1988
α_2	Proportion hunted	uniform(0, 1)	0.5(0.29)	after 1988
$\sigma_{p,i}^{-2}$	St. dev. i th stage/sex class	gamma(0.001, 0.001)	1(31.65)	$i = \{1, 2, 3\}$
$\sigma_{d,1}$	St. dev. abundance data	uniform(0, 500)	250(144.33)	1969 – 1994
$\sigma_{d,2}$	St. dev. abundance data	uniform(0, 500)	250(144.33)	1995 – 2010

4.1.5 Choosing alternatives for management

Fitting the model to monitoring data provided us with information about the current and past states of the system. Partitioning the model variance into components arising from the observation system and components arising from the model of the population process allowed us to make forecasts, that is, predictions of the future state of the population accompanied by rigorous estimates of uncertainty. Forecasts are based on the predictive process distribution of the population size (See Hobbs and Hooten, pages 196-201 for details). We compared the distribution of the posterior predictive values to a range of values that reflected the park's management objectives and calculated the probability of meeting those goals given different potential levels of culling.

We used the full hierarchical model to forecast the overwinter elk population size for three years into the future, conditioned on all the data observed up to the present year. For example, we used data collected through 2008 and subsequently forecasted elk abundance in 2009, 2010 and 2011. We used the same model fitting procedure each subsequent year after 2008. The final year of analysis consisted of data observed through 2015, with forecasted elk abundance in 2016, 2017, and 2018.

To demonstrate the utility of these forecasts, we further compared two years of analysis that reflected different states of the elk population. The forecasts from our hierarchical model answered the question of whether or not population growth was outside the target range of 600-800 elk, with attendant uncertainty. However, in an adaptive management framework, it is not enough to know whether a target was achieved; we need to know annually how management actions could influence the population trajectory and if those actions will meet our goals.

A fundamental question for elk management in RMNP is whether and how many elk should be culled to meet management objectives. We have annually provided managers with information since 2008 to help answer these questions by forecasting the future state

of the population under multiple alternatives for culling: 0, 25, 50, or 75 adult females. We calculated the probability that the population size would be within the target given each level of culling. The highest probability of obtaining the target goal would naturally inform the choice of management action, including “no action” when culling was set to 0 within the forecasts.

4.2 Results

Marginal posterior distributions of the total elk population size during winter tracked the observed increase and decline in elk abundance (Figure 4.4). The population increased until the mid 1980s, when it appeared to stabilize at approximately 1,000 animals. The population decreased steadily after the early 2000s (Figure 4.4), a decline that has several potential causes, including harvest, the movement of large numbers of elk to new winter range areas, and disease (Monello et al., 2014; National Park Service, 2007). Beginning in 2002, a shift in the winter distribution of elk with increased use of areas east of the Estes Valley was evident. Concerns of an over-abundant elk population in the Data Analysis Unit that contains RMNP led Colorado Parks and Wildlife to increase hunting licenses for females (Figure 4.5). The adult female harvest from the mid 1990s nearly tripled in the early 2000s, peaking at just over 400 elk in 2006. In addition, between 2009 and 2011 a total of 130 female elk were removed from the population by culling, including 71 elk that were euthanized and used for research (Monello et al., 2013), in order to reduce and maintain elk numbers at the low end of the population objective. No culling has occurred since 2011.

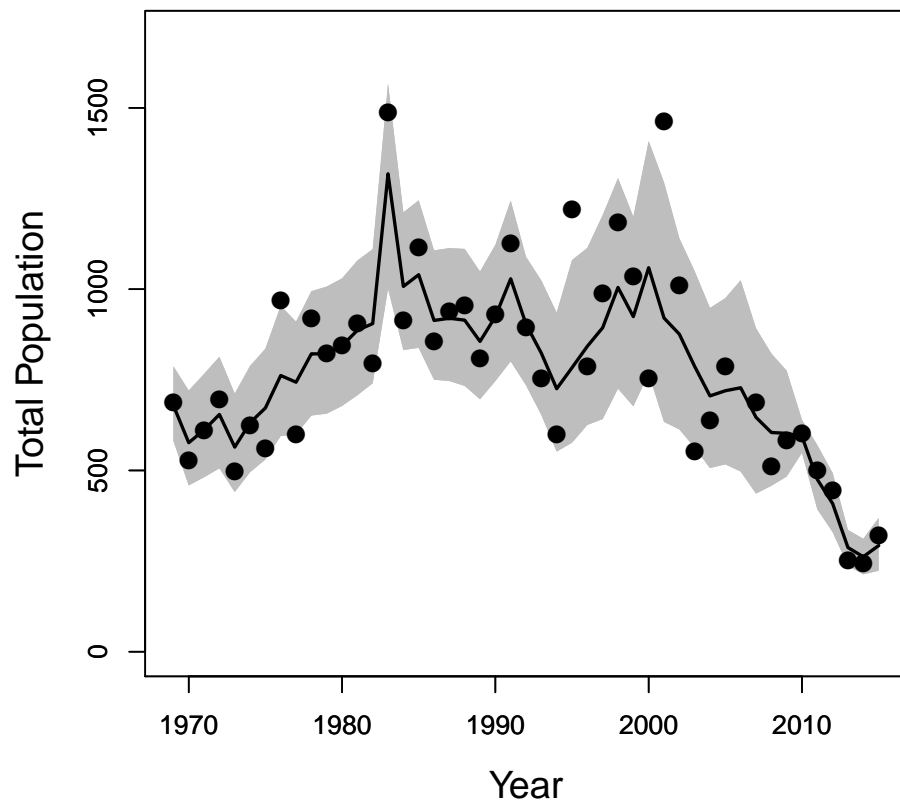


Figure 4.4: The median (black line) and 95% quantiles (grey shaded region) for the posterior distributions of the true elk population size on the winter range in Rocky Mountain National Park during 1969 to 2015 shows the variability of the population size over time. The black dots represent the observed elk population sizes.

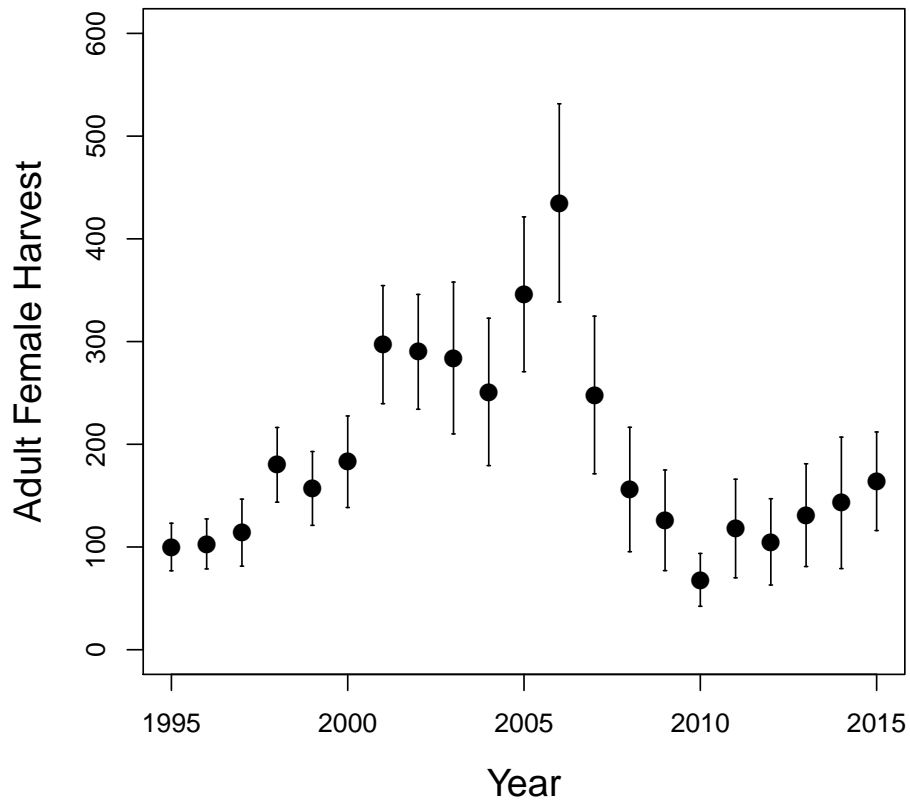


Figure 4.5: Mean harvest of adult females from 1995-2015 (dots with 95% Bayesian credible intervals) for Data Analysis Unit 20 reported by Colorado Parks and Wildlife, increased steadily during 1995-2005 before declining to approximately the same level as in 1995. There was an increase of adult female harvest in the early 2000s, peaking in 2006.

The median estimated average recruitment (μ_r) from which all of the time varying recruitment parameters were drawn was 0.29 (BCI = 0.25, 0.33) calves per adult female elk surviving to census. This was much lower than the average adult female recruitment of 0.464 used in the prior distribution (Table 4.1), that was reported by Raithel et al. (2007) using data from multiple elk populations throughout the Rocky Mountain region. A simple linear regression line of recruitment versus time has a decreasing trend such that the average

recruitment decreased by 0.0028 (equal tailed BCI for the coefficient = $-0.0040, -0.0015$) calves per adult female per year (Figure 4.6).

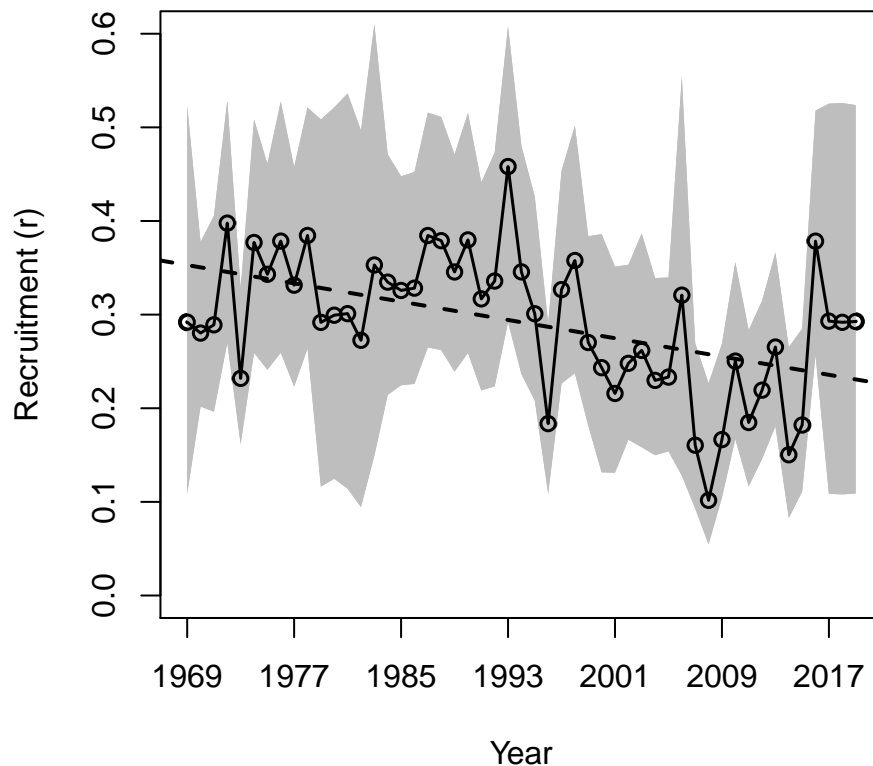


Figure 4.6: Open circles give the mean of the posterior distribution and grey shaded areas are 95% equal-tailed credible intervals of annual recruitment rates, r_t , the number of offspring produced per yearling and adult female that survive to their first census during year t . The dashed line gives the fit of the simple linear regression of the average annual recruitment rates (r_t) versus time (t).

The proportion of animals 8 months old that survived to 20 months of age, had a median juvenile survival of $s_1 = 0.49$, with an equal tailed Bayesian credible interval (BCI = $0.22, 0.78$). Adult males had a median probability of survival of 0.91 (BCI = $0.79, 0.99$), in the absence of hunting. Adult female survival, 0.94 (BCI = $0.93, 0.95$), was slightly greater than survival of males and resembled survival in other unhunted elk populations (Brodie

et al., 2013). The process variance parameters, on the log scale, of the three stage/sex classes were greater for males than for adult females. There typically is greater variability for male survival in ungulates (Gaillard et al., 2000).

Table 4.2: The marginal posterior means, standard deviations, medians, and 95% equal-tailed credible intervals for all parameters included in the model. Note that $\sigma_{p,i}$ are on the log scale.

Parameter	Definition	Mean	St. Dev.	Median	2.5%	97.5%
s_1	Juvenile survival	0.49	0.14	0.49	0.22	0.78
s_2	Adult female survival	0.94	0.00	0.94	0.93	0.95
s_3	Adult male survival	0.91	0.05	0.92	0.79	0.99
m	Proportion male juveniles	0.49	0.05	0.49	0.40	0.59
μ_r	Ave. Recruitment	0.29	0.02	0.29	0.25	0.33
σ_r	St. dev. recruitment	0.10	0.02	0.10	0.05	0.14
α_1	Proportion hunted 1968-1989	0.12	0.09	0.10	0.01	0.33
α_2	Proportion hunted 1990-2015	0.07	0.05	0.07	0.00	0.18
$\sigma_{p,1}$	St. dev. juveniles	0.11	0.09	0.08	0.02	0.36
$\sigma_{p,2}$	St. dev. adult females	0.18	0.06	0.17	0.08	0.33
$\sigma_{p,3}$	St. dev. adult males	0.55	0.10	0.54	0.37	0.76
$\sigma_{d,1}$	St. dev. abundance data	124.65	34.59	122.13	63.45	201.11
$\sigma_{d,2}$	St. dev. abundance data	240.75	80.68	236.64	86.74	415.40

Culling activities ceased after 2011 because forecasts indicated the population size was lower than the objective of 600-800 elk, although still within the broad objective of 200-800 elk (National Park Service, 2007). The abundance of elk using the winter range of RMNP was estimated at 294 (BCI=223,369) individuals in 2015. The decline in abundance appears to have stabilized from 2013 to 2015 (Figure 4.4), with the elk population consistently estimated in the high 200s.

The observed elk abundance data is compared with the forecasts and their 95% Bayesian credible intervals (Figure 4.7). Credible intervals on forecasts overlapped the one-to-one line where forecasts equal observations during 15 out of 18 years, indicating considerable skill in our model. Credible intervals on forecasts expanded with an increasing forecast horizon,

suggesting that forecasts beyond three years would have limited predictive value (Figures 4.7B and 4.7C).

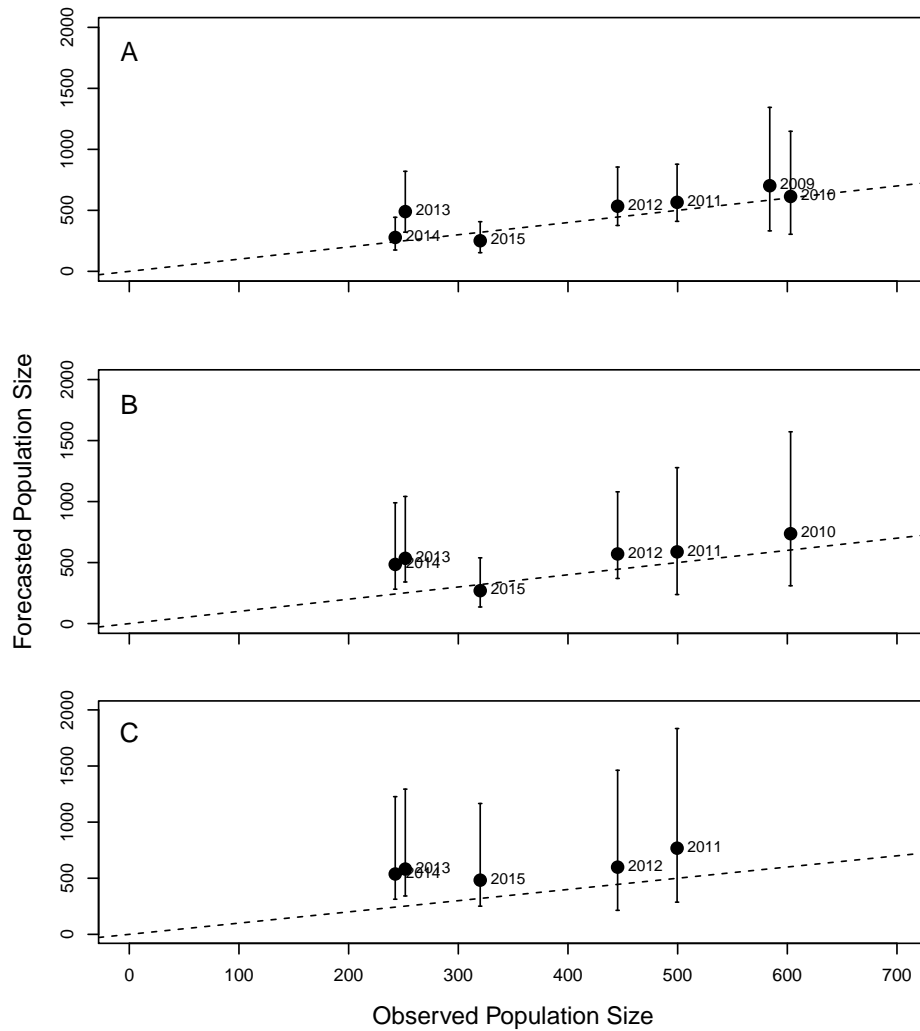


Figure 4.7: Observed population estimates are plotted against forecasts with corresponding 95% Bayesian Credible Intervals for one (figure A), two (figure B) and three (figure C) years into the future. The dashed line indicates the one-to-one line in which the forecasted population size equals the observed population size.

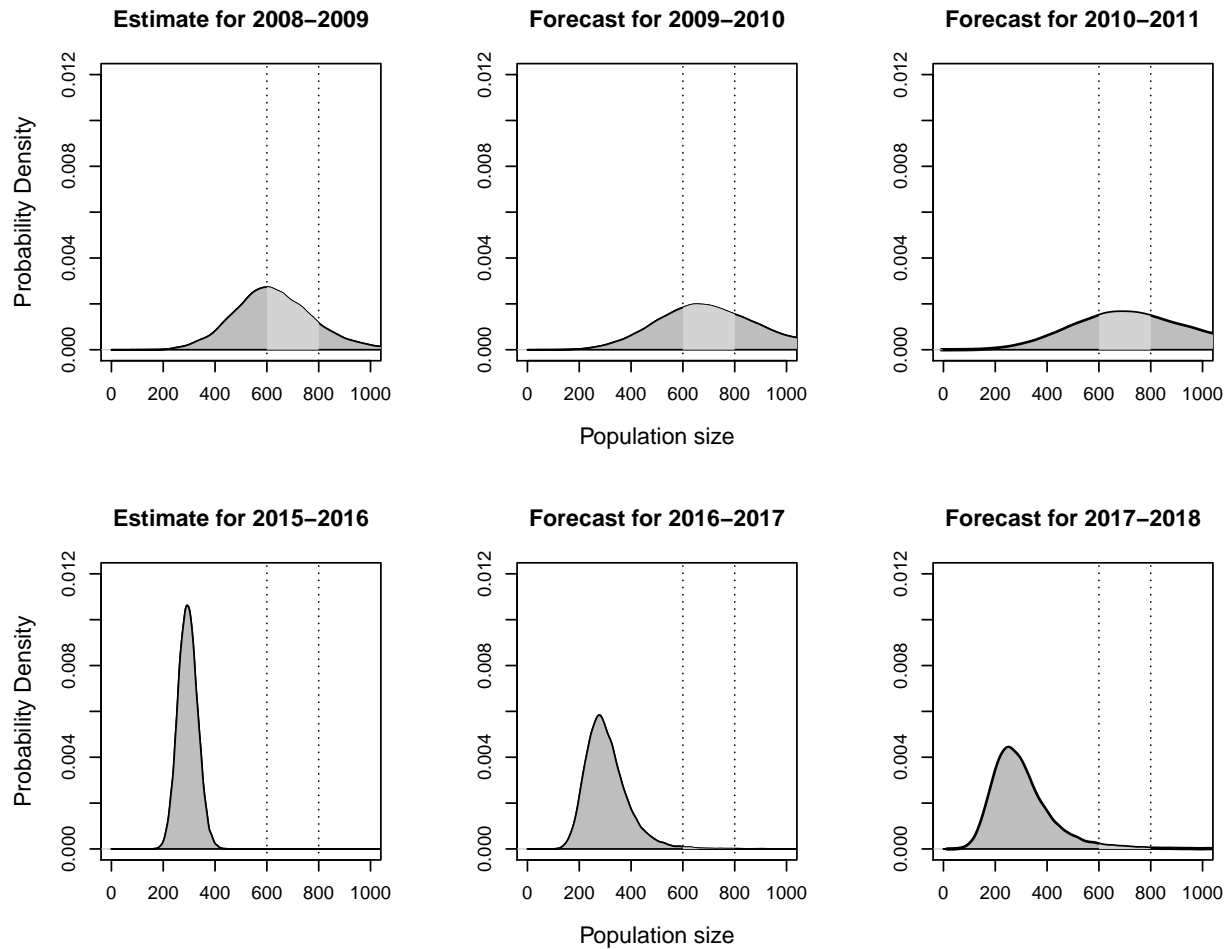


Figure 4.8: The marginal posterior distributions (left column) and posterior predictive distributions (center and right columns) for elk abundance during 2008-2010 and 2016-2018. The vertical dashed lines indicate the target range for the elk population of 600-800 elk, and the light shaded grey regions are the probability that the population is within the target range.

The marginal posterior distribution of the population size for the current year and the posterior process distributions for future years can be seen in Figure 4.8. In 2008, the estimate of the population size was 611 (BCI = 338, 972) elk, which was more than double the population sizes estimated in 2015. This estimate was within the target range, however, forecasts indicated that if no animals were culled, the number of elk would likely increase to 701 elk in 2009, 742 elk in 2010, and 777 elk in 2011 (see Table 4.3). We calculated the

probability that the population size would be above, within, and below the target range of 600-800 elk in future years. The choice to cull 0, 25, 50 or 75 animals all had roughly equivalent probabilities of maintaining the population within the target range for the three subsequent forecasts into the future. However, under the no cull management action, there was a much greater probability of the population increasing above the 800 elk threshold than culling individuals. Because management was primarily concerned with overabundance, the NPS culled a total of 46 elk in 2009, including 32 individuals that were euthenized for a study on chronic wasting disease (Monello et al., 2013). The elk population size and forecasts have been estimated well below the target range after 2011, therefore no elk have been culled since that year.

Table 4.3: Forecasts for different culling regimes conditioned on observed data through 2008, with corresponding 0.025 and 0.975 equal tailed Bayesian credible intervals for overwinter abundance. The probability that elk abundance is below, within, and above the target range is shown in the rightmost three columns.

Cull	Year	N	.025	.975	P <	P in	P >
0	2009	701	347	1240	0.30	0.37	0.32
	2010	742	331	1451	0.27	0.32	0.41
	2011	777	312	1680	0.25	0.28	0.47
25	2009	655	302	1186	0.39	0.36	0.25
	2010	686	282	1364	0.36	0.32	0.33
	2011	713	258	1572	0.33	0.28	0.38
50	2009	626	277	1141	0.45	0.34	0.21
	2010	651	253	1320	0.42	0.31	0.28
	2011	675	228	1502	0.39	0.27	0.34
75	2009	600	258	1109	0.50	0.31	0.19
	2010	618	229	1267	0.47	0.29	0.24
	2011	640	203	1454	0.44	0.26	0.30

4.3 Discussion

Deterministic, simulation models have been used to support decisions on management of natural resources since the early 1970's (Walters and Gross, 1972; Holling, 1973; Maynard Smith, 1974; May and Oster, 1976; May, 1976; Freedman, 1980; Otto and Day, 2007). These types of models have been criticized because confidence in their predictions led to notable failures in policy and management (Pilkey and Pilkey-Jarvis, 2007). Reliable use of models to support decisions requires honest estimates of uncertainty.

Combining models with monitoring data along with the results of designed studies of processes in the Bayesian framework allows the outputs of models to be properly tempered by rigorous estimates of uncertainty arising from multiple sources. Such assimilation adds value to monitoring data by providing inference on the true, unobserved states of systems being managed. Informed management requires three components: reliable data on the past and current state of the system being managed, clear objectives for management, and a way to evaluate the ability of alternative actions to achieve those outcomes. Bringing these components together in a coherent framework for modeling is vital for successful adaptive management as it was originally formulated by Walters (1986). The monitoring data of elk in RMNP provides an ideal system for implementing adaptive management because the NPS has invested in a long-term time series of data relative to key resource decisions—how to best manage the elk population. In addition, innovative science was used to formulate appropriate management goals. Having clearly stated objectives for the winter range population size enabled us to evaluate possible management outcomes.

By employing the Bayesian framework, we were able to partition the variability inherent in the biological and management processes from the uncertainties that arise through sampling and estimation error. We estimated demographic parameters such as recruitment and survival from observations of the population of elk over time, and then used these parameters to predict the future abundance of elk accompanied by an honest assessment of uncertainty.

These forecasts were assessed by comparing them to the estimated observed number of elk as these data became available (Figure 4.7). Results indicated that the forecasts from a single year into the future accurately predicted the observed number of elk and emphasizes the importance of taking management actions on this time scale. Forecasts further into the future became less accurate and appeared to overestimate the observed population size. This is likely an artifact of the long time series of data with high population sizes early in the time series that inflate the forecasted population sizes later in the time series .

Under the policy of natural regulation in the absence of significant predation, elk abundance grew throughout the 1970s. The population size appears to have stabilized at approximately 1,000 elk during the 1980s (Hess, 1993). Hobbs et al. (1982) estimated a carrying capacity on the elk winter range of 1,481 elk for one year and 991 elk for a second year based on the energy and nitrogen availability of forage in the ecosystem. Lubow et al. (2002) estimated a similar carrying capacity of 1,069 elk using a demographic projection model paired with a sightability model using the ground and aerial data collected in the 1990s. The consistency of the carrying capacity estimates provides support that one should expect the population in the winter range to vary around 1,000 elk under natural regulation without substantial predation. Density dependence has been shown to decrease fecundity and increase age at first reproduction in large herbivores (Singer et al., 2007; Sæther, 1997; Clutton-Brock et al., 1987; Sauer and Boyce, 1983), which are suggested as the primary mechanisms for this trend (Lubow et al., 2002; Coughenour, 2002). The estimates of recruitment demonstrate a paradoxical trend regarding density dependence in this population. One would expect that recruitment should increase as the population size decreases, if a density dependent feedback mechanism were present. However, this has not occurred for the elk in RMNP despite the possible density dependence demonstrated during high population years (Lubow et al., 2002; Coughenour, 2002).

Recent estimates are considerably lower than might be expected given the predominant narrative of overabundant elk in RMNP (Hess, 1993). However, trends during the last three

years suggest that the population may be stabilizing after an extended period of decline (Figure 4.4). The decline in elk numbers after 2008 not only guided management actions, but also helped spur additional research to discover the role of chronic wasting disease, emigration, and novel patterns of elk winter range use in RMNP (*unpublished data*). Past modeling work had found that elk numbers were relatively stable across winter and that surveys in February were likely a good indicator of elk conditions on the winter range (Lubow et al., 2002; Singer et al., 2007). New monitoring data contradicts this pattern and new survey methods are being used to assess the variability of the elk use of the winter range.

High levels of harvest by hunters outside of the park during the early 2000s likely contributed to the current, reduced abundance of the elk population (Figure 4.5). However, harvest rates have been relatively constant since 2008. If the harvest remains at the current level, the elk abundance may rebound, particularly since the decadal decline in elk coincided with peaking harvest rates. However, it is important to note that large, unanticipated changes in parameters such as adult female survival or emigration may alter the relationship between hunter harvest outside the park and population trajectory (Clutton-Brock et al., 2002; Petersburg et al., 2000; Nielsen et al., 1997; Labonté et al., 1998; Monello et al., 2014). An important future step could be to assess a range of hunter harvest quantities within the hierarchical model by setting multiple limits for each stage/sex category and calculating the predicted abundance given alternative harvests in order to provide guidance to Colorado Parks and Wildlife for setting harvest objectives. Altering harvest quantities could also be useful in other managed systems (Nichols et al., 1995; Johnson et al., 2002).

The approach we illustrate could be useful for managing national parks throughout the world. Investment in monitoring data is justified in terms of its value for determining if the state of parks is consistent with goals for park ecosystems. Our illustration shows how a Bayesian approach can be applied to gain insight from monitoring data by evaluating alternatives for management in terms of the ability to meet goals for the future. Wide use of these methods will require collaboration among scientists and managers. Investment in

training decision makers in the foundations of Bayesian methods would likely offer substantial dividends.

Our experience in this example and others (Hobbs et al., 2015; Raiho et al., 2015) suggests that monitoring past states of park ecosystems provides sufficient information to support forecasts with a limited horizon, usually less than four years. Forecasts are necessarily short term because there is an accumulation of uncertainty for each subsequent year that causes the credible intervals to expand rapidly, the further into the future that we try to forecast. This limitation reinforces the need for adaptive management over a frequent cycle: monitoring data are used to improve the model, the model is used to enhance decisions. Multiple iterations of this cycle increase understanding of the processes creating variability in the system being managed and provide a science-based foundation for decisions that can be explained to an engaged public.

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APPENDICES

5.1 Appendix Chapter 2

5.1.1 Directed acyclic graph

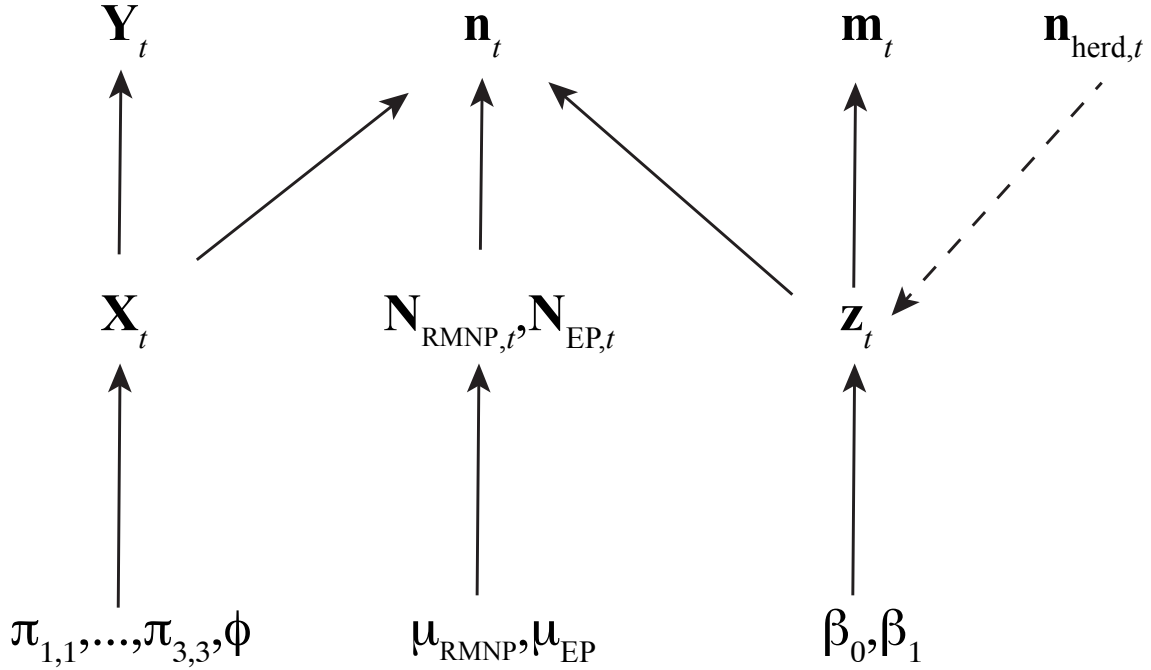


Figure 5.1: Directed Acyclic Graph (DAG) of the full model shows the hierarchical relationships between the data (top row), latent states (middle row), and hyperparameters (bottom row). The solid arrows represent dependent relationships and the dashed line represents relationships derived from random variables. Data includes weekly telemetry locations (\mathbf{Y}_t), monthly average ground counts (\mathbf{n}_t), monthly resights of collards (\mathbf{m}_t), herd size counts within a subset of monthly ground counts ($\mathbf{n}_{\text{herd},t}$). Latent states include true locations of collared individuals (\mathbf{X}_t), the population size during the t th week of winter in Rocky Mountain National Park ($\mathbf{N}_{\text{RMNP},t}$) and in the town of Estes Park ($\mathbf{N}_{\text{EP},t}$), and the calibrated number of marks (\mathbf{z}_t). Hyperparameters include movement probabilities (π), weekly probability of survival (ϕ), overwinter average population size (μ) and coefficients in the calibration model for adjusting the number of resights (β_0, β_1).

5.1.2 Model statement, full posterior, and joint distributions

Combining the components of the model statement described above, the full posterior and joint distributions are:

$$[\mathbf{N}, \mathbf{X}, \mathbf{z}, \pi_{1,1}, \dots, \pi_{3,3}, p_s, p_v, p_d, \beta_0, \beta_1, \mu | \mathbf{Y}, \mathbf{m}, \mathbf{n}] \propto \prod_{t=2}^T \prod_{i=1}^{r_t} [\mathbf{y}_{i,t} | 1, g_d(p_s, p_v, p_d, \phi, \mathbf{x}_{i,t})] \quad (43)$$

$$\times [\mathbf{x}_{i,t} | 1, g_p(\phi, \pi_{1,1}, \dots, \pi_{3,3}, \mathbf{x}_{i,t-1})] \quad (44)$$

$$\times [m_t | z_t, \beta_0, \beta_1] \quad (45)$$

$$\prod_{\tau} [n_{\tau} | N_{\tau}, \mathbf{X}_{\tau}, z_{\tau}] [N_{\tau} | \mu] \quad (46)$$

$$\times [\mu] [\beta_0] [\beta_1] [\pi_{1,1}, \dots, \pi_{3,3}] [\phi] [p_s] [p_v] [p_d], \quad (47)$$

where

$$g_d(p_s, p_v, p_d, \mathbf{y}_{i,t}) = \mathbf{D}_{i,t} \mathbf{x}_{i,t} \quad (48)$$

$$g_p(\phi, \pi_{1,1}, \dots, \pi_{3,3}, \mathbf{x}_{i,t-1}) = \mathbf{\Theta} \mathbf{x}_{i,t-1} \quad (49)$$

The parameters in the posterior and joint distributions include the overwinter average population size (μ), the monthly population sizes (\mathbf{N}), the matrix of true telemetry locations (\mathbf{X}), the matrix of calibrated resights (\mathbf{Z}), coefficients for the calibration model (β_0, β_1), movement probabilities ($\pi_{11}, \dots, \pi_{33}$) that are used in the matrix $\mathbf{\Theta}$, detection probabilities (p_s, p_v, p_d) that are used in the matrix \mathbf{D} , and weekly survival probability (ϕ). The data include the observed telemetry locations for the I marked individuals during the T weeks of winter (\mathbf{Y}), the resighted marks (\mathbf{m}) and mean of the ground surveys (n_{τ}) during \mathcal{T} weeks that are a subset of the T telemetry sampling occasions.

5.1.3 Parameter results - tables and plots

Here we present tables of summary statistics of model parameters across all years of the study, for movement and detection. We also present plots of prior and posterior distributions for model parameters of overwinter average population sizes in Rocky Mountain National Park (μ_{RMNP}) and the town of Estes Park, CO (μ_{EP}), and weekly survival (ϕ) for all years of the study. We also plot prior and posterior distributions of movement probabilities for the final year of surveys (2015). Prior distributions are markedly different than posterior distributions which shows that the data are informing the posterior distributions of model parameters.

Table 5.1: Estimated detection probabilities for the data model of the telemetry observations across all years of the study. Probabilities are defined as p_s is the probability of detecting a telemetry collar, p_v is the probability that a location was obtained given a detection, and p_d is the conditional probability that a collared individual is in the study region given that the collar was detected and location information was observed. The right two column headings represent the 0.025 and 0.975 quantiles of the marginal posterior distributions.

Year	Parameter	Definition	Mean	Median	SD	0.025	0.975
2011	p_s	detected	0.833	0.833	0.012	0.808	0.856
	p_v	location	0.999	0.999	0.001	0.995	1.000
	p_d	study area	0.996	0.996	0.002	0.990	0.999
2012	p_s	detected	0.644	0.644	0.009	0.626	0.661
	p_v	location	0.999	1.000	0.001	0.998	1.000
	p_d	study area	0.989	0.989	0.003	0.984	0.993
2013	p_s	detected	0.542	0.542	0.008	0.527	0.557
	p_v	location	1.000	1.000	0.000	0.998	1.000
	p_d	study area	0.977	0.977	0.004	0.969	0.983
2014	p_s	detected	0.437	0.437	0.008	0.421	0.453
	p_v	location	0.999	1.000	0.001	0.998	1.000
	p_d	study area	0.985	0.985	0.003	0.978	0.991
2015	p_s	detected	0.479	0.479	0.008	0.463	0.495
	p_v	location	0.999	1.000	0.001	0.998	1.000
	p_d	study area	0.999	1.000	0.001	0.997	1.000

Table 5.2: Movement probabilities estimated for all years of the study (Figure 2). All probabilities are notated such that the location during the t th time period is represented with an i and the location at time $t + 1$ is represented with a j (π_{ij}). The right two columns are the 0.025 and 0.975 quantiles of the marginal posterior distributions.

Year	Probabilities	Mean	Median	SD	0.025	0.975
2011	π_{11}	0.87	0.87	0.02	0.84	0.90
	π_{12}	0.97	0.98	0.02	0.92	1.00
	π_{21}	0.94	0.94	0.03	0.85	0.99
	π_{22}	0.80	0.80	0.03	0.74	0.84
	π_{32}	0.67	0.71	0.24	0.16	0.99
	π_{33}	0.96	0.97	0.03	0.90	1.00
2012	π_{11}	0.85	0.85	0.01	0.82	0.87
	π_{12}	0.99	0.99	0.01	0.97	1.00
	π_{21}	0.80	0.80	0.03	0.73	0.87
	π_{22}	0.86	0.86	0.01	0.84	0.89
	π_{32}	0.58	0.61	0.22	0.12	0.93
	π_{33}	0.97	0.97	0.01	0.95	0.99
2013	π_{11}	0.89	0.89	0.01	0.88	0.91
	π_{12}	0.91	0.92	0.04	0.84	0.98
	π_{21}	0.53	0.53	0.05	0.44	0.62
	π_{22}	0.83	0.83	0.01	0.80	0.86
	π_{32}	0.42	0.42	0.05	0.32	0.52
	π_{33}	0.85	0.85	0.01	0.82	0.87
2014	π_{11}	0.83	0.83	0.01	0.80	0.86
	π_{12}	0.97	0.97	0.02	0.92	0.99
	π_{21}	0.62	0.62	0.04	0.53	0.70
	π_{22}	0.83	0.83	0.01	0.80	0.86
	π_{32}	0.53	0.53	0.06	0.41	0.64
	π_{33}	0.82	0.82	0.02	0.78	0.85
2015	π_{11}	0.88	0.88	0.01	0.86	0.90
	π_{12}	0.97	0.97	0.02	0.91	0.99
	π_{21}	0.59	0.59	0.05	0.50	0.69
	π_{22}	0.85	0.85	0.01	0.83	0.88
	π_{32}	0.34	0.34	0.06	0.23	0.46
	π_{33}	0.83	0.83	0.02	0.80	0.86

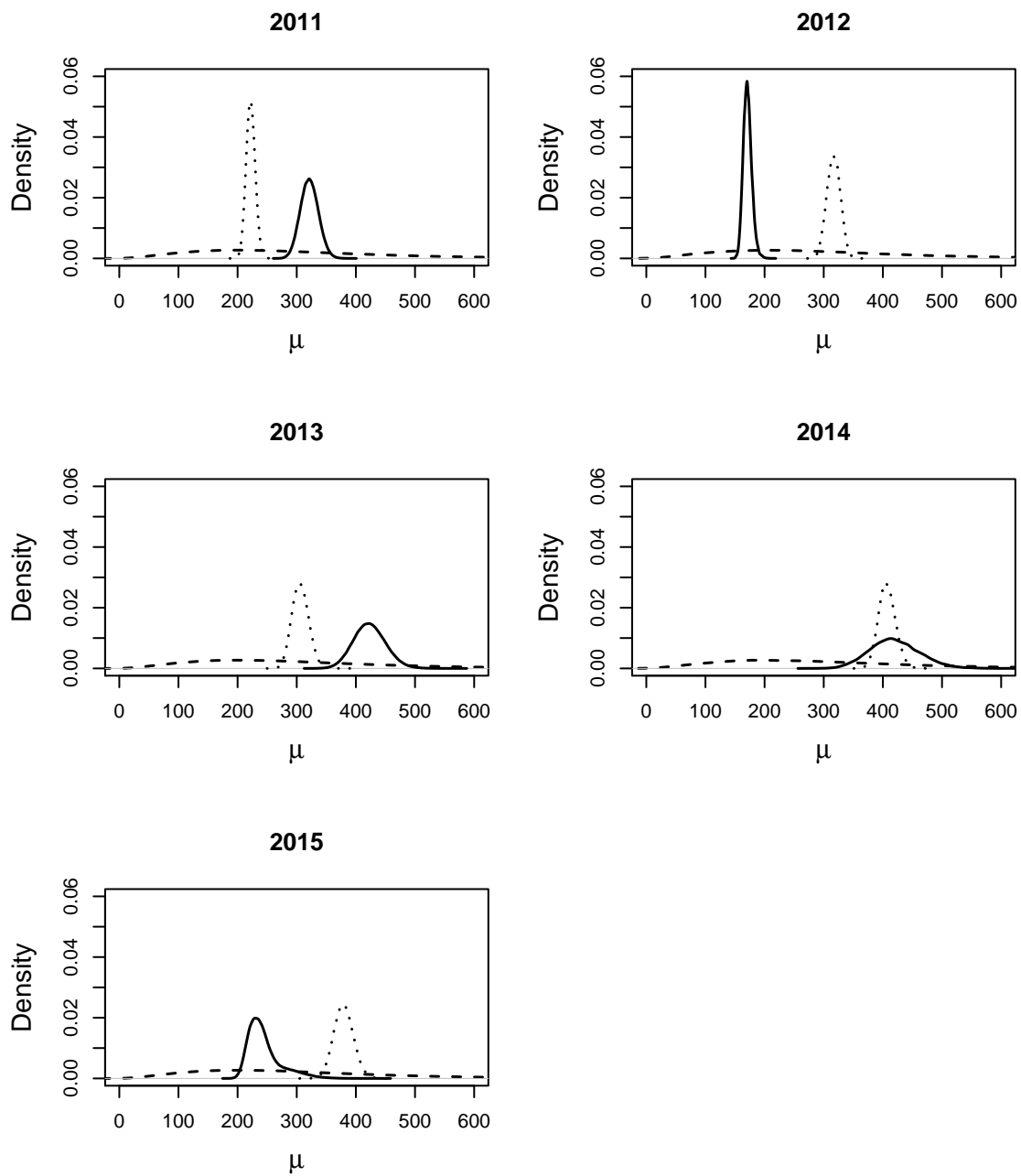


Figure 5.2: Marginal posterior distributions of the overwinter population size of elk in Rocky Mountain National Park (solid line) and the town of Estes Park (dotted line). Vague prior distributions were used for the population size in RMNP and EP (dashed line).

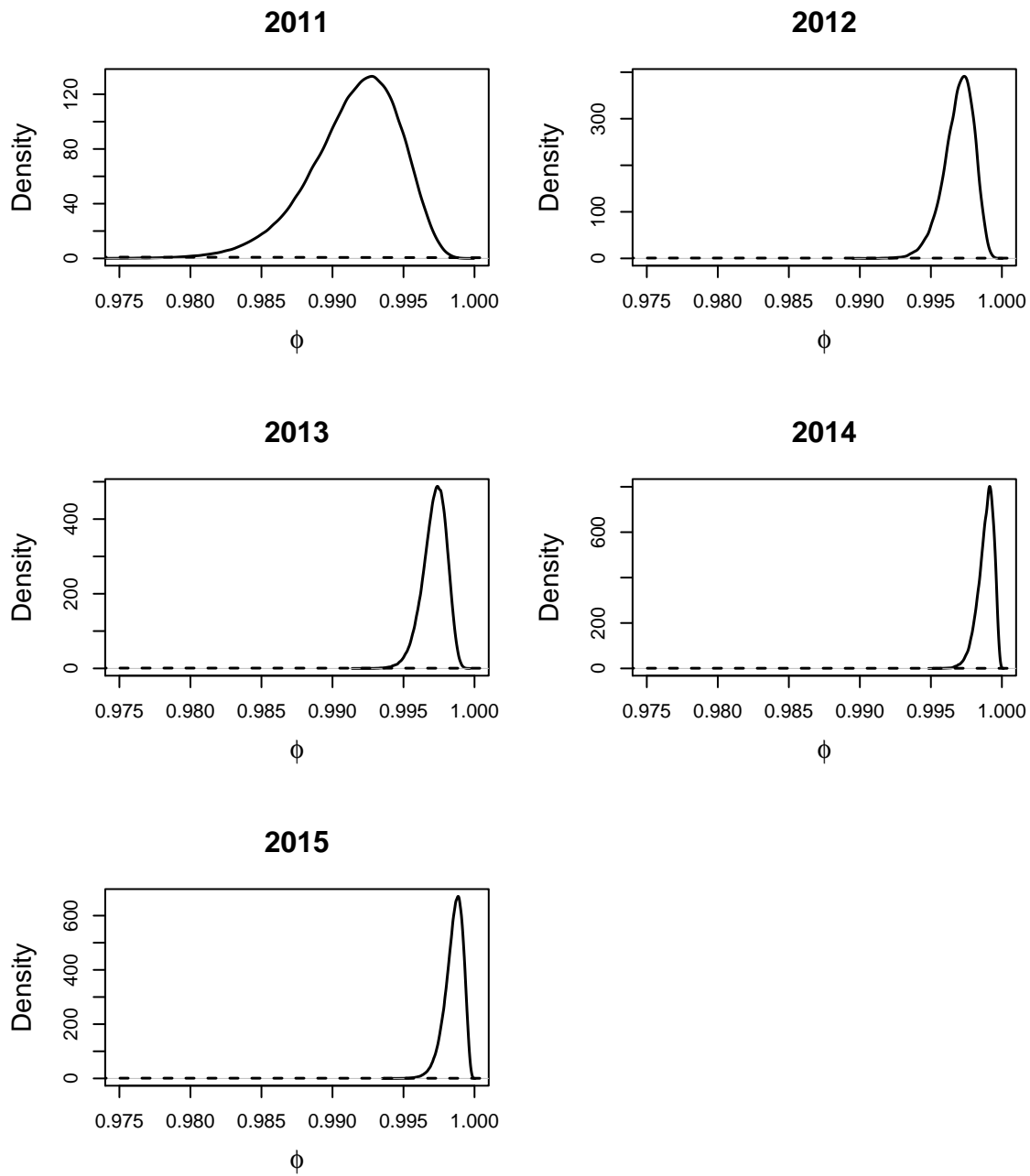


Figure 5.3: Flat prior distributions (dashed lines) and posterior distributions (solid lines) for the weekly survival parameter (ϕ) for all years of the study.

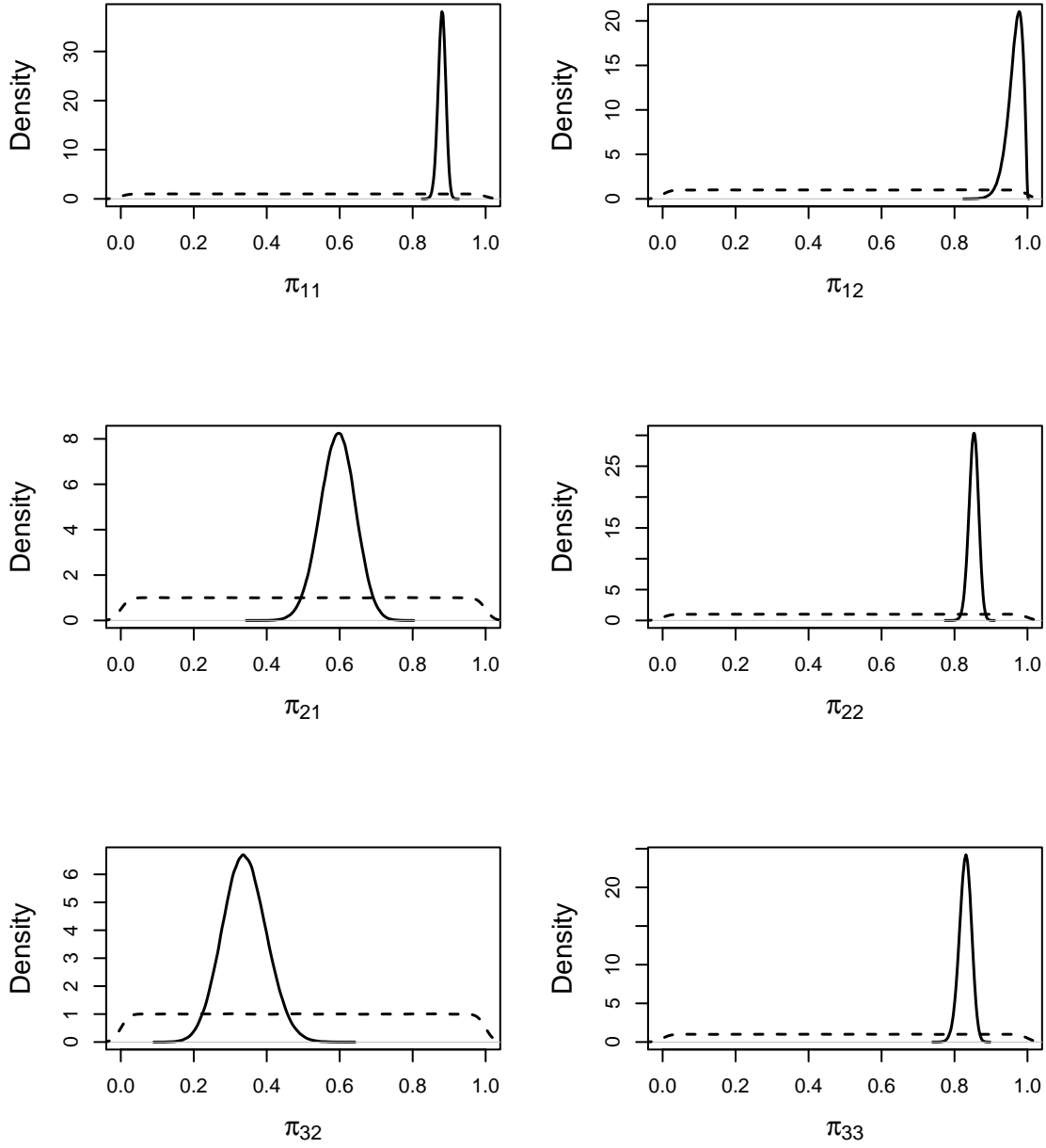


Figure 5.4: Prior distributions (dashed lines) and posterior distributions (solid lines) for the conditional movement probabilities from the the transition matrix (Θ) in the process model (see Figure 2).

5.2 Appendix Chapter 3

5.2.1 Model statement, full posterior, and joint distributions

Here, we describe the components of the classification model. The three models presented in the text follow the same multinomial structure for the likelihood. To be concise, we present a full model, with posterior and joint distributions for the empirical Bayes model only. The data consist of counts of groups of individuals, summed across $i = 1, \dots, I$ surveys during the $t = 1, \dots, T$ years, denoted $\mathbf{y}_{i,t}$, for 4 sex/stage classes and an additional unknown category. The group level data that were subsetting according to adult female and juvenile herds are denoted by x_{k_t} . Parameters include the “true” proportions of each stage/sex ($\boldsymbol{\pi}_t$), the proportion of unknown classifications ($p_{z,t}$), the proportions of the calf/cow herds ($\boldsymbol{\omega}_t$), and prior distributions for these parameters. Thus, the full model statement is given by

$$\mathbf{y}_{i,t} \sim \text{multinomial}(N_{i,t}, \mathbf{p}_t), \quad (50)$$

$$\boldsymbol{\pi}_t \sim \text{Dirichlet}(\boldsymbol{\alpha}_t), \quad (51)$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}^*_t / \alpha_0, \quad (52)$$

$$\alpha_0 = \sum_{j=1}^J \alpha^*_j, \quad (53)$$

$$\alpha^*_j \sim \text{gamma}(.001, .001), \quad (54)$$

$$p_{z,t} \sim \text{uniform}(0, 1), \quad (55)$$

$$\mathbf{x}_{k_t} \sim \text{multinomial}\left(\sum_{j=1}^J x_{j,k,t}, \boldsymbol{\omega}_{t+1}\right), \quad (56)$$

$$\boldsymbol{\omega}_1 \sim \text{Dirichlet}(23, 71, 4, 2), \quad (57)$$

$$\boldsymbol{\omega}_{t+1} \sim \text{Dirichlet}(1, 1, 1, 1), \quad (58)$$

where $N_{i,t} = \sum_{j=1}^{J+1} y_{j,i,t}$, and

$$\mathbf{p}_t = \begin{pmatrix} \pi_{1,t} - \omega_{1,t} \times p_{z,t} \\ \pi_{2,t} - \omega_{2,t} \times p_{z,t} \\ \pi_{3,t} - \omega_{3,t} \times p_{z,t} \\ \pi_{4,t} - \omega_{4,t} \times p_{z,t} \\ p_{z,t} \end{pmatrix}. \quad (59)$$

We combine all components of the model into the full posterior and joint distributions.

$$\left[\mathbf{\Pi}, \boldsymbol{\alpha}^*, \mathbf{p}_z, \mathbf{\Omega} | \mathbf{Y}, \mathbf{X} \right] \propto \prod_{t=2}^T \prod_{i=1}^{I_t} [y_{i,t} | \boldsymbol{\pi}_t, p_z, \boldsymbol{\omega}_{t-1}] \prod_{k=1}^{K_t} [\mathbf{x}_k | \boldsymbol{\omega}_t] \times \quad (60)$$

$$[\boldsymbol{\omega}_t] \left[\boldsymbol{\pi} | \boldsymbol{\alpha}^* \right] \left[\boldsymbol{\alpha}^* \right] [p_z] \times \quad (61)$$

$$\left[\mathbf{y}_{i,1} | \boldsymbol{\alpha}_1^* \right] [\mathbf{x}_{k_1} | \boldsymbol{\omega}_1] [\boldsymbol{\omega}_1] \quad (62)$$

5.2.2 Summary statistics tables

Table 5.3: Summary statistics of the marginal posterior distributions of the proportions of all classes ($\boldsymbol{\pi}$) from 2012 through 2016 for elk in Rocky Mountain National Park using the empirical Bayes approach.

Year	Parameter	Mean	Median	SD	.025	.975
2012	π_1	0.153	0.152	0.012	0.133	0.179
	π_2	0.577	0.578	0.014	0.548	0.602
	π_3	0.061	0.060	0.006	0.052	0.075
	π_4	0.209	0.208	0.008	0.195	0.226
2013	π_1	0.181	0.181	0.005	0.172	0.190
	π_2	0.616	0.616	0.006	0.604	0.628
	π_3	0.066	0.066	0.003	0.060	0.072
	π_4	0.138	0.138	0.004	0.129	0.146
2014	π_1	0.179	0.179	0.005	0.168	0.190
	π_2	0.595	0.595	0.007	0.581	0.609
	π_3	0.073	0.073	0.004	0.066	0.080
	π_4	0.154	0.153	0.005	0.143	0.164
2015	π_1	0.159	0.159	0.007	0.147	0.173
	π_2	0.591	0.591	0.008	0.574	0.608
	π_3	0.063	0.063	0.004	0.056	0.072
	π_4	0.186	0.186	0.005	0.176	0.197
2016	π_1	0.201	0.201	0.005	0.190	0.212
	π_2	0.587	0.587	0.007	0.574	0.600
	π_3	0.066	0.066	0.003	0.060	0.073
	π_4	0.146	0.146	0.005	0.137	0.155

Table 5.4: Summary statistics of the marginal posterior distributions of the proportions of all classes ($\boldsymbol{\pi}$) from 2012 through 2016 for elk in Rocky Mountain National Park using the out-of-sample approach.

	Parameter	Mean	Median	SD	.025	.975
2012	π_1	0.152	0.152	0.006	0.141	0.164
	π_2	0.561	0.561	0.008	0.545	0.576
	π_3	0.065	0.065	0.004	0.058	0.073
	π_4	0.222	0.222	0.006	0.210	0.235
2013	π_1	0.183	0.183	0.011	0.163	0.205
	π_2	0.615	0.615	0.012	0.590	0.639
	π_3	0.054	0.054	0.006	0.044	0.066
	π_4	0.148	0.147	0.006	0.137	0.160
2014	π_1	0.188	0.188	0.012	0.166	0.213
	π_2	0.576	0.576	0.014	0.548	0.602
	π_3	0.078	0.078	0.008	0.065	0.094
	π_4	0.158	0.158	0.007	0.144	0.173
2015	π_1	0.153	0.153	0.007	0.140	0.168
	π_2	0.597	0.597	0.009	0.579	0.615
	π_3	0.055	0.055	0.003	0.049	0.062
	π_4	0.194	0.194	0.006	0.182	0.207
2016	π_1	0.204	0.203	0.006	0.192	0.215
	π_2	0.577	0.577	0.007	0.563	0.591
	π_3	0.068	0.068	0.004	0.061	0.075
	π_4	0.151	0.151	0.005	0.141	0.161

Table 5.5: Summary statistics of the marginal posterior distributions of the proportions of all classes ($\boldsymbol{\pi}$) from 2012 through 2016 for elk in Rocky Mountain National Park using the ignoring (trim) approach.

	Parameter	Mean	Median	SD	.025	.975
2012	π_1	0.148	0.148	0.005	0.138	0.159
	π_2	0.546	0.546	0.008	0.531	0.561
	π_3	0.066	0.066	0.004	0.059	0.074
	π_4	0.239	0.239	0.007	0.227	0.252
2013	π_1	0.182	0.182	0.006	0.170	0.194
	π_2	0.526	0.526	0.008	0.510	0.542
	π_3	0.063	0.063	0.004	0.056	0.071
	π_4	0.228	0.228	0.007	0.215	0.242
2014	π_1	0.183	0.183	0.007	0.169	0.198
	π_2	0.519	0.519	0.009	0.501	0.537
	π_3	0.084	0.084	0.005	0.074	0.094
	π_4	0.214	0.214	0.008	0.199	0.229
2015	π_1	0.153	0.153	0.005	0.143	0.163
	π_2	0.560	0.560	0.007	0.546	0.574
	π_3	0.065	0.065	0.003	0.058	0.072
	π_4	0.222	0.222	0.006	0.211	0.234
2016	π_1	0.202	0.202	0.006	0.191	0.214
	π_2	0.577	0.577	0.007	0.564	0.591
	π_3	0.067	0.067	0.004	0.060	0.074
	π_4	0.153	0.153	0.005	0.143	0.163

5.3 Appendix Chapter 4

5.3.1 Bayesian Modeling

Here, we provide a schematic treatment of Bayesian forecasting models. We begin by defining the term *state variable* to mean a numerical quantity describing a condition of interest at a given point in time. Examples of state variables might include the number of invasive plants per unit area, the levels of particulates in the air, the prevalence of a disease, the size of an ungulate population, or the levels of dissolved nutrients in streams. We will use the notation z_t to mean the *true*, unobserved value of the state variable at time t .

It is rarely possible to observe the true state perfectly. Observations often need to be calibrated to correct for bias. Sampling variation usually needs to be quantified, simply because it is not possible to observe all instances of the state variable of interest in all possible locations. To deal with this uncertainty, we define a stochastic model of monitoring data as

$$[y_t | z_t, \boldsymbol{\theta}_d]. \quad (63)$$

The notation reads the probability distribution of an observation (y_t) conditional on the true value of the state (z_t) that gave rise to the observation and the parameters describing the observation process ($\boldsymbol{\theta}_d$), including the uncertainty that arises from calibration and sampling.

The purpose of collecting monitoring data is to quantify how the state variable changes over time. We define a model for the temporal change in the state variable as

$$[z_t | z_{t-1}, \boldsymbol{\theta}_p] \quad (64)$$

where the notation reads the probability distribution of the true state at time t conditional on its value at time $t - 1$ and parameters ($\boldsymbol{\theta}_p$). Included in $\boldsymbol{\theta}_p$ are parameters in a deterministic model portraying the temporal trajectory of the state and, notably, an estimate of process

variance, which includes all of the influences on the state variable that are not included in the deterministic model. Equation 64 is customarily called a *process model*. It can be mechanistic or empirical or a blend of the two and can be regarded as the hypothesis for explaining how the ecological system works.

By assembling the process model (Equation 64) and data model into a single expression using Bayes Theorem and the laws of probability for factoring joint distributions we obtain

$$[\boldsymbol{\theta}_d, \boldsymbol{\theta}_p, \mathbf{z} | \mathbf{y}] \propto \underbrace{\prod_{t \in \mathcal{T}} [y_t | \boldsymbol{\theta}_d, z_t]}_{\text{data model}} \underbrace{\prod_{t=2}^T [z_t | \boldsymbol{\theta}_p, z_{t-1}] [\boldsymbol{\theta}_d] [\boldsymbol{\theta}_p] [z_1 | \boldsymbol{\theta}_p]}_{\text{process model}} \quad (65)$$

where \mathcal{T} is the set of observations in a time series of monitoring data.⁵ Equation 65 is a Bayesian hierarchal model, also called a Bayesian state space model (Berliner, 1996; Newman et al., 2006; Calder et al., 2010). The model is hierarchical because it contains a model of the data linked probabilistically to a model representing the processes giving rise to the data. The left hand side of the proportional symbol (\propto) is the posterior distribution. It informs us about the probability distributions of all of the unobserved parameters and true states by updating prior information model parameters (including the possibility that not much is known) with observed monitoring data. All sources of uncertainty are combined in the model (equation 65) in a statistically coherent way.

5.3.2 Process model, full posterior, and joint distributions

Here, we bring together all of the components of the process model described in the text (see the Methods section, Chapter 4). The true, unobserved number of elk \mathbf{n} within three stage and sex classes are modeled as a function of survival \mathbf{s} , fecundity \mathbf{r} , the proportion of male juveniles m , the true number of hunted elk h_{true} within a winter range subset ($\boldsymbol{\alpha}$), the

⁵There can be "gaps" in the time series of observations. Missing data are handled in the same way all other unknown quantities in the Bayesian framework.

number of culled elk (c) before (pre) and after (post) census, as well as the proportion of the number of adult females that have been subject to fertility treatments (I) described in ??.

Variability in the process model is accounted for using the multivariate normal distribution and subsequent variances on the log scale (Σ_p). The true number of hunted elk (h_{true}) is estimated using the estimates of the observed number of hunted elk (\mathbf{h}_{obs}) and their standard errors (σ_{hunt}). The total population size N_{total} at time t is calculated from the process model as the sum of the estimates in each stage/sex category and thus, the true proportion of elk in each category is \mathbf{p}_t .

$$\log(\mathbf{n}_t) \sim \text{multivariate normal}(\log(\boldsymbol{\mu}_t), \Sigma_p) \quad (66)$$

$$h_{\text{true},i,t} \sim \text{gamma}\left(\frac{h_{\text{obs},i,t}^2}{\sigma_{\text{hunt},i,t}^2}, \frac{h_{\text{obs},i,t}}{\sigma_{\text{hunt},i,t}^2}\right) \quad (67)$$

$$\begin{pmatrix} \mu_1 \\ \mu_2 \\ \mu_3 \end{pmatrix}_t = \begin{pmatrix} 0 & r_t s_2^{1/3} & 0 \\ (1-m)s_1 & s_2 & 0 \\ ms_1 & 0 & s_3 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \\ n_3 \end{pmatrix}_{t-1} - \alpha_j \begin{pmatrix} h_{\text{true},1} \\ h_{\text{true},2} \\ h_{\text{true},3} \end{pmatrix}_{t-1} - \begin{pmatrix} r_t c_{\text{pre}} \\ c_{\text{post}} \\ 0 \end{pmatrix}_{t-1} - \begin{pmatrix} r_t I_n I_p s_2 \\ 0 \\ 0 \end{pmatrix}_{t-1} \quad (68)$$

$$N_{\text{total},t} = \sum_{i=1}^3 n_{i,t} \quad (69)$$

$$\mathbf{p}_t = \left(\frac{n_{1,t}}{N_{\text{total},t}}, \frac{n_{2,t}}{N_{\text{total},t}}, \frac{n_{3,t}}{N_{\text{total},t}} \right)' \quad (70)$$

We combine all components of the model into the full posterior and joint distributions. Model parameters described above are conditioned on observed data consisting of total population size counts (\mathbf{y}_1), classification counts in three distinct stage and sex categories (\mathbf{Y}_2), and the observed number of hunted elk (\mathbf{H}_{obs}).

$$[\mathbf{n}, \mathbf{s}, \boldsymbol{\alpha}, m, \mathbf{r}, \mu_r, \sigma_r, \mathbf{H}_{\text{true}}, \boldsymbol{\sigma}_p, \boldsymbol{\sigma}_d | \mathbf{y}_1, \mathbf{Y}_2, \mathbf{H}_{\text{obs}}] \propto \prod_{t=2}^T \left[y_{1,t} | N_{\text{total},t}, \sigma_{d_j,t}^2 \right] \left[\mathbf{y}_{2,t} | \sum_{i=1}^3 y_{2,i,t}, \mathbf{p}_t \right] \times \quad (71)$$

$$[n_t | \mu_{t-1}, \Sigma_p] [h_{\text{obs},t} | h_{\text{true},t}, \sigma_{\text{hunt},t}^2] [r_t | \mu_r, \sigma_r] \times \quad (72)$$

$$[n_1 | y_{1,1}, Y_{2,1}] [s] [\alpha] [m] [\mu_r] [\sigma_r] [\sigma_p^2] [\sigma_d^2] \quad (73)$$

5.3.3 Fertility

Bradford and Hobbs (2008) designed a model and simulated population management strategies contrasting fertility control (both lifelong and year-long) with culling of adult female elk, for maintaining population growth rates in a stage structured model. In 2008, 47 elk were treated with contraception and the number of infertile elk for the subsequent few years were estimated given the initial number of females treated. The model simulation suggested that the use of fertility treatments could lead to extinction, even with the use of adaptive management, and that culling provided a more efficient method of population reduction to meet target goals if population size needed reduction. The park service opted to use culling as the predominant method of population size management as implemented in the Elk and Vegetation Management Plan beginning in 2009.

The influence of fertility treatments during the years 2008 through 2011 are included in the model by specifying the number of treated females ($I_{n,t}$) and the proportion of those females that are actually infertile ($I_{p,t}$) and consequently should not be included in the number of female elk surviving to reproduce since they are unable to do so. The number of infertile female elk for the years in which there is data, are $\{47, 26, 13, 4\}$ which could potentially influence the overall growth of the population.

Data model likelihoods

Multiple likelihoods were used to model the data because multiple sampling methods were employed, including aerial surveys, ground surveys and a combination of these census

methods. For the first 25 years of the study from 1969-1994, when there was no clear survey sampling design, we combine the estimation and sampling error using a single constant variance parameter $\sigma_{d,1}^2$ and specify the likelihood for the data as $N_{\text{obs},t} \sim \text{normal}(N_{\text{total},t}, \sigma_{d,1}^2)$, where $N_{\text{total},t} = \sum_{i=1}^3 n_{i,t}$, which is derived from the three categories of the state space process model.

Estimation error was provided for the single annual aerial surveys that occurred from 1995-2010 in the form of a standard error estimated through bootstrapping (Lubow et al., 2002). Hence, the elk abundance during those years are modeled with an additional level of structure that allows us to separate estimation error from sampling error. A single constant variance parameter ($\sigma_{d,2}^2$) was used for the estimation error. Thus,

$$\lambda_t \sim \text{normal}(N_{\text{total},t}, \sigma_{\text{obs},t}) \quad (74)$$

$$N_{\text{obs},t} \sim \text{normal}(\lambda_t, \sigma_{d,2}^2) \quad (75)$$

where λ_t represents the mean from the distribution from which the total population arises and $N_{\text{total},t}$, as well as $N_{\text{obs},t}$ are defined above.

For the years 2011-2015, variation in the observation error that incorporates both sampling and estimation uncertainty can be estimated directly from the data because multiple surveys were used. The likelihood for the abundance data uses the observed variation across the multiple surveys within each winter season described as

$$N_{\text{obs},t} \sim \text{normal}(N_{\text{total},t}, \sigma_{\text{obs},t}^2). \quad (76)$$